III. *On the Leaves of Calamites* (Calamocladus *Section*).*

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[Plates 3–5.]

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Introduction.

The last few decades have seen enormous additions to our knowledge of the structure of fossil plants, and we have now a very complete acquaintance with the stems, roots, and fructifications of a considerable number of Coal Measure genera. But although this is the case, comparatively little is yet known about the structure of their foliar organs. Renault's classic researches brought to light many interesting leaves, particularly from the Autun district; but scarcely any petrified leaves from the English deposits have been studied in detail. This, no doubt, constitutes a very serious gap in our knowledge of the Palæozoic flora,

* Part of a Walsingham Medal Essay, 1909.

and it is my intention to endeavour to make detailed studies of leaf structure in the principal groups of Coal Measure plants.

The subject has important bearings in several directions, apart from a merely descriptive interest. It is now generally recognised that the leaves of plants growing in different habitats almost universally exhibit adaptations correlated with the physical conditions of their surroundings, and definite types of structure are developed according to the amount of water and light supplied. A considerable mass of evidence on this subject is being accumulated by the study of modern plants. It seems perfectly legitimate to use this evidence in the reverse manner, and from the characters of leaf structure to draw deductions as to the climate and conditions of growth in Coal Measure times. Leaves show these modifications more strikingly than any other parts of the plant, and hence a detailed knowledge of fossil leaves is of great importance in the discussion of the climatology of the Coal Measure period, and incidentally in regard to the question of the formation of coal.

Most of the recent work in Fossil Botany has been concerned almost entirely with morphological and phylogenetic considerations, and little attention has been given to the physiological significance of the tissue studied.* The present paper is an endeavour to deal with the leaf tissues from the standpoint of physiological anatomy, in so far as this is possible in petrified material. This should provide data for climatological considerations, and at the same time, perhaps, throw some light on questions of the origin and development of plant structures.

The present paper deals with some of the leaves (Calamocladus section) of the genus Calamites. A number of leaves showing slightly different types of structure will be described, and an attempt made to correlate some of them with the species known from impressions. It is hoped that this paper will add to our knowledge in the field outlined by Dr. D. H. SCOTT in the conclusion of his 'Studies in Fossil Botany,' which appeared while this work was in progress. He says: "The subject of the biology and ecology of fossil plants, as illustrated especially by their physiological anatomy, offers a wide and promising field of research. Such biological studies will be of the greatest intrinsic interest, and will also throw a new and welcome light on the problems of evolution."†

HISTORICAL.

Much has been written on the subject of Calamite-leaf impressions, and a considerable number of species have been described. These have been divided into two classes—probably corresponding to separate orders—the Calamocladus group and

* Some papers from the latter point of view have, however, been recently published, *e.g.*, one by Prof. SEWARD "On the so-called Phloem in Lepidodendron," another by Prof. WEISS on the Parichnos in the same group.

† SCOTT ('09), p. 663.

the Annularia group. The former is described by Prof. SEWARD as follows:—"Branched or simple articulated branches bearing whorls of uni-nerved linear leaves at the nodes; the leaves may be either free to the base or fused basally into a cup-like sheath (*e.g.*, GRAND' EURY'S Calamocladus). The several acicular linear leaves or segments which are given off from the nodes spread out radially in an open manner in all directions; they may be either almost at right angles to the axis or inclined at different angles. Each segment is traversed by a single vein and terminates in an acuminate apex."* The Annularias are characterised by the same author thus:—"Opposite branches are given off in one plane from the nodes of a main axis; the leaves are in the form of narrow sheaths divided into numerous and unequal linear or narrower lanceolate segments, each with a median vein. The segments in each whorl appear to be spread out in one plane, very oblique to the axis of a branch, instead of spreading radially in all directions; the lateral segments are usually longer than the upper and lower members of a whorl."† I have not yet been able to discover any petrified specimens of leaves clearly referable to the Annularia group.

In the English Coal Measure deposits five species of Calamocladus have been discovered. Dr. KIDSTON gives the following list in his table showing the distribution of fossil plants‡: *C. equisetiformis* (Schl.), *C. longifolius* (Sternb.), *C. grandis* (Sternb.), *C. charæformis* (Sternb.), *C. lycopodioides* (Zeiller). With the exception of *C. charæformis* all are recorded from the Lower Coal Measures, the division from which all our petrified specimens are derived.

Very little, however, has been written on the subject of leaf structure. Graf SOLMS-LAUBACH stated in 1891 that no leaf-bearing branch of the group showing structure had yet been found.§ WILLIAMSON,|| however, in his tenth Memoir figured a small object from Halifax which was undoubtedly a section through a badly preserved Calamite leaf bud, with five leaves in a whorl. He stated¶ that it is "a section of the upper extremity of either a fruit or a young shoot with pentamerous phyllomes alternating in contiguous verticils," but was acquainted with nothing corresponding to it, and in the description of Plates calls it "a pentamerous fruit (?) from Halifax." I have not found any specimens which agree exactly with it, but it may be compared with sections through buds figured on Plate 5, figs. 5, 6, 8. In 1895 the late Mr. T. HICK published a paper on the structure of the leaf of Calamites,** in which he described some slides now in the Manchester Museum. He gives a good brief description of several leaves, which I attribute to the Charæformis type, but he was at a loss to account for their small size. He remarks that his leaves in their size and form resemble those of Chara, but he does not seem to have been acquainted with the impression species *C. charæformis* (Sternb.). He did not notice any

* SEWARD ('98), p. 333.

† *Idem*, p. 337.

‡ KIDSTON ('94).

§ SOLMS-LAUBACH ('91), p. 322.

|| WILLIAMSON ('80), Plate 15, fig. 12A.

¶ *Idem*, p. 502.

** HICK ('95).

definite traces of stomata, but recognised all the other main points, neglecting, however, to emphasise the Calamitean features of the stems attached to his leaves.

In 1898, Prof. SEWARD shortly re-described and figured some of HICK'S leaves, pointing out that the structural characters suggested that the plant lived in a fairly damp climate. He was the first to notice the stomata.* Dr. SCOTT, in the first edition of his 'Studies' (1900), observed that a young stem bearing these leaves could not be recognised as being really that of a Calamite, and suggested it might be the peduncle of a strobilus.† He figured and very briefly described a new specimen from his own collection which, though it shows clearly the arrangement of the leaves, is not very well preserved. This completes the list of previous work on leaf structure. It will be noticed that only one type or species of leaf had been described when the present work was commenced, and much remained to be cleared up even with regard to that species.

THE MATERIAL.

In spite of the abundance of Calamite stems in petrified material, specimens showing their leaves have proved to be extremely rare. This is probably due to the very delicate nature of the leaf tissues, for, as will be seen later, they were of such a kind that the conditions necessary for their preservation must have been exceptional. Almost all my specimens are derived from the same horizon, the Halifax Hard Bed of the Lower Coal Measures. Calcareous nodules from the Lancashire localities sometimes contain leaves, but in most cases they are not sufficiently well preserved to be of any value.

Calamite leaves are so small that they have, for the most part, escaped the attention of collectors, and most of the slides I have used were originally prepared to show sections of Calamostachys cones. Except in two cases I have not had the advantage of serial sections, but as the same section very often cuts through two or more whorls in different planes, this drawback has been lessened.

Some of my slides have been prepared for me by Mr. J. LOMAX, but several of the more important ones have been borrowed from other collections. Dr. D. H. SCOTT and Mr. D. M. S. WATSON have lent me slides from their collections, while I am indebted to Prof. WEISS for the loan of slides from the Manchester Museum, and to Prof. OLIVER for others from the Collection at University College, London. I am particularly indebted to these gentlemen, as without their interest and help the present work would have been impossible. I have only been able to find two slides containing Calamite leaves in the Williamson Collection at the British Museum, and only a few of the slides in the Binney Collection at the Sedgwick Museum, Cambridge, were sufficiently well preserved to be of much value. The following is a list of the slides used :—

From the Manchester Museum : Nos. R 7, 14, 945 ; Q 164, 167, 168, 169, 233.

* SEWARD ('98), pp. 330–332.

† SCOTT ('00), p. 37. This does not appear in the second edition, *cf.* SCOTT ('08), p. 40.

From Dr. SCOTT's collection: Nos. 900, 171, 2263, and 2455.*

From Prof. OLIVER, University College, London: Nos. F 1, H 1 B, H 1 C, H 2.

From Mr. D. M. S. WATSON's collection: Nos. A 64, A 89, A 189.

From the Binney Collection (Sedgwick Museum, Cambridge): AB 1, AB 4, AB 5, AB 11, 191.

Slides obtained from Mr. J. LOMAX: C 1–14.

Most of the slides show young shoots with leaves attached to them, and usually many sections of isolated leaves are also seen. The detached leaves are of less value owing to the difficulty in making out the direction and position in which they are cut, but are often very valuable in supplying details of structure. The leaves are usually imbedded in clear calcareous mineral substance, which is often remarkably free from fragmental plant remains. Associated with them we find many young stems of Calamites, some Lepidodendron leaves, and the usual Stigmarian rootlets.

A large number of specimens are found in which the tissues are not well preserved, and seem to have shrivelled before petrification. This appearance is first noticeable in palisade tissue, where the filament-like cells contract, and appear like single threads or walls. At the same time the outline of the section alters owing to contraction, and the epidermal cells collapse. These specimens are by far the commonest; an example is shown in Plate 5, fig. 8, and the specimen figured by Dr. SCOTT is also in this condition.† In other cases the delicate cells of the palisade tissue have become disorganised and decayed before preservation, this being especially the case in some of the larger types of leaf.

HICK mentions cases in which he found a well-marked carinal canal below the vascular bundle. I have not found the slightest trace of such a canal in any moderately well preserved specimen, and those which he observed were almost certainly only cavities produced by the decay of the tissues, for the leaf in which he figures the canal is very imperfect. It will be seen later, when the xylem is described, that it is so small in amount and of such a nature as to render the formation of carinal canals, comparable to those formed in the stem, very improbable. I do not think that canals were formed in any of the Calamite leaves.

THE CHARÆFORMIS TYPE (I).

The commonest petrified Calamite leaves are small linear falcate structures borne in whorls of four on slender twigs. They often occur associated with small stems and cones of the *Calamostachys Binneyana* type. As will be shown later, they bear considerable resemblance to the impression-species *Calamocladus charæformis*.

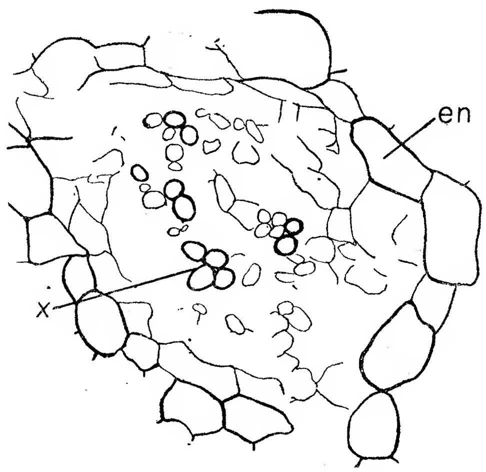
The structure of the twigs bearing leaves of this type differs considerably from that of older stems, and in view of this some doubt was formerly cast on their Calamitean nature. It may be well, therefore, to describe them in detail.

* In order to distinguish these slides the letter S is prefixed before the number when reference is subsequently made to them.

† SCOTT ('08), fig. 14, p. 40.

The Twigs.

A transverse section through a young twig shows a small stele in the centre, surrounded by parenchymatous cortical tissue. It will be convenient to consider the stele separately. Its appearance seems to vary considerably, depending on the age of the twigs and the plane of the section. In the earliest stages, the stele, as seen in transverse section (S 171), is solid, with thin-walled pith in the centre. Through the internodes the xylem appears to consist of four groups of from 3–6 tracheides with scalariform thickening surrounded by the thin-walled ground tissue (see text-fig. 1)



TEXT-FIG. 1.—Camera Lucida Drawing of Transverse Section of Stele seen in one of the Youngest Stems. S 171. The xylem tracheides (*x*) with some remains of the thin-walled tissue (phloem ?) are seen. On the outside there is a ring of large cells, probably representing the endodermis (*en*). × 250.

The phloem cannot be clearly distinguished. The stele is surrounded by a single layer of large clear cells with thicker walls, possibly representing the endodermis. A section (R 945) passing through a node presents a different appearance (Plate 3, fig. 1). The xylem now appears to have increased somewhat in amount, and forms a solid cylinder of tracheides in the centre of the stem. Some of these show a distinct tendency to concentric arrangement. The section was cut rather obliquely, but two of the four vascular strands which run out to the leaves at the node are well seen. Surrounding the xylem there is a zone of cells with thin walls, but with no definite arrangement. They appear to be of the nature of elongated parenchyma, and some of them may perhaps represent phloem. The endodermis-like cells are again present. The stems with structure of this type are about 0·8 mm. in diameter.

In older twigs the xylem increases considerably in amount, and becomes more or less ring-shaped in transverse section. This is seen in several sections (S 171, R 945, H 2). Some of these (S 171) show that the tracheides are in groups separated by medullary rays, but the latter are often very indistinct. A good section through one

of these older twigs is seen in S 900 (Plate 3, fig. 2), which is cut just above a node. The xylem here appears to form a hollow cylinder four cells thick, with four medullary rays marking out the original bundles. Some of the cells are very regularly arranged, but others are oblique owing to proximity to the node. A leaf-trace bundle is seen on one side. The phloem in this and the succeeding slide is not clearly differentiated, but seems to be composed of very thin-walled cells. A similar stage is well shown in Plate 3, fig. 3 (slide H 1*b*), which is cut just above a node. The stems in this stage are only about 1 mm. in diameter. It will be noticed that they differ from adult stems in the small size of the medullary rays and in the absence of carinal canals. It has been suggested that some stems of this type were really the peduncles of cones. Apart from the fact that they are much more slender than the axes of the Calamostachys cones present in the same slide, there is little evidence for or against this hypothesis. A still larger twig is seen in R 945 (Plate 3, fig. 4). This is nearly 2 mm. in diameter, and is surrounded by several small leafy shoots, as though they had been produced as a whorl of branches from it. There is a large pith-cavity in the centre, and this is surrounded by xylem, which is now definitely split up into bundles by the broadening medullary rays. It seems that in some places secondary rays were being formed, but the structure is not very clear. There are no obvious carinal canals, but below some of the xylem groups occur small cavities, caused by the disintegration of the tissue. These may, perhaps, represent the beginning of the canals. The phloem, again, can scarcely be distinguished, but is probably represented by a small number of thin-walled cells external to the xylem, which are badly preserved. Here, as in many other fossil plants, the identification of this tissue is a point of considerable difficulty. No old shoots have been found connected with leaves, but several sections show stems, probably of the same type as those just described, in which the wedge-shaped xylem groups are still further separated, and carinal canals are developed (H 1*c*) (see Plate 3, fig. 5).

Longitudinal sections through the twigs are not very common, but several have been found (Plate 4, fig. 12). The xylem is differentiated quite near the apex, and the tracheides or vessels show scalariform thickening. The xylem strands of the stele are seen to alternate in position between the nodes, and the arrangement seems to be just the same as in older stems. In young twigs the xylem is unbroken, but as the age of the twig increases the protoxylem becomes pulled out, and the thickening bands of the tracheides separate. This process goes on till the protoxylem ultimately breaks down and the carinal canal is formed. Practically all stages in the formation of these canals may be studied in the longitudinal sections. (It is seen just beginning in C 13 (*a*), which shows a stem about 8 mm. in diameter, while in Q 164 the change has gone much further, and several rows of tracheides have broken down. The latter specimen was described and figured by HICK ('93), but the figure does not show the protoxylem clearly. In this stage it is comparable with Dr. SCOTT's figure in the 'Studies,' p. 23.) The phloem, as seen in longitudinal

section, consists of very long cells with thin walls. No structures like sieve-plates can be made out, but the tissue is often badly preserved and the cells very narrow.

The cortex usually forms a conspicuous feature in these young stems. In some cases it seems to be marked off from the stele by a layer of large cells with thicker walls (see text-fig. 1, Plate 3, figs. 1 to 3), but in many of the sections it is extremely difficult to determine the boundary between them. The cortex is roughly divisible into an inner and an outer part. The cells of the inner portion (S 171, 2) have thinner walls and are for the most part considerably elongated. The lumen of the cell is sometimes filled with a dense black carbonaceous substance resembling that found in the leaves and bracts (Plate 3, figs. 2 and 4). In the outer part of the cortex the cells have rather thicker walls and are less elongated. Among them larger cells with thick walls and a deep brown colour occur (fig. 2), but the cells are mostly thin-walled parenchyma. The two regions of the cortex are by no means sharply delimited, and the variation in structure in different specimens is very considerable. On the outside of the stem there was a narrow epidermis.

We thus see that though the sections through young twigs present an appearance differing somewhat from that of the older stems previously known, yet their structure is, in the main, very similar. There can be no doubt as to the Calamitean affinities of the leaves described here. At the same time it is probable that there were differences in structure between twigs of different species, as will be noted later. It is possible, too, that the main stem in its early stages may have been also completely different in structure from the twigs, while those bearing cones may have had another structure. Mr. D. M. S. WATSON has lent me a section through a very young Calamite stem about 0·5 mm. in diameter which is very unlike those described above. It has a small stele in the centre which is divided into three parts. Each part is seen as a little fan-shaped group of about 20 tracheides with a distinct carinal canal on the inside (Plate 3, fig. 6). The stele thus presents a very distinct triarch structure. There is no pith, and the phloem appears to be almost absent. There is a broad cortex, the inner part of which is characterised by cells with dense black contents, and probably some of these performed the function of phloem (see later, p. 78). There are no leaves attached to this stem, but a transverse section of a rather badly preserved leaf is seen in the material near it. This stem may be, of course, only a twig of another species of Calamite, but it may be suggested that it was the embryonic stage of a large stem. JEFFREY* has shown that the first shoots of *Equisetum hiemale* and *E. limosum* differ in structure from the subsequent ones, and it is possible that a difference of this kind existed among the Calamites.

The structure of these small stems provided several interesting comparisons with that of modern Equisetums. JEFFREY† has described the structure of the young

* JEFFREY ('99).

† *Idem.*

shoot of *Equisetum limosum*, in which the stele in the upper internodes possessed a triarch structure, being composed of three collateral bundles surrounded by a common endodermis. This stage may be compared with that of the young stem just described. Again, in the same species and in *E. hiemale* "the central cylinder of the first shoot makes its appearance as an unbroken tube of reticulate tracheides. There are no typical protoxylem elements, although the internal tracheides are formed first." This type of structure is almost exactly what we get in the Calamite twigs. Prof. JEFFREY'S description might, in fact, have been written about the structure seen in section S 900. Another comparison can be drawn between the Calamite twigs and the young Equisetum stems with reference to the number of leaves in the whorls. In the former this is usually four or six, but from impression-specimens we see that the number was often much greater in thicker stems. A similar state of affairs exists in the Equisetum stems. The early leaf-whorls may have only two or three members, while this number becomes considerably increased in the mature stem.

The Leaves.

The internodes of the twigs vary somewhat in length, but in most of the specimens described below they are about 1 mm. long. The leaves of successive whorls alternate in position, as might be anticipated from the course of the vascular strands. The alternation is well seen in transverse sections through the twigs near their apex, in which two or three whorls are seen cut through in different positions (*cf.* Plate 3, fig. 1 ; Plate 5, fig. 8). There are usually four leaves in a whorl, and they are arranged symmetrically. However, though four is the usual number in most of the specimens examined, it is not invariable. One section (F 1) shows two young shoots which have five leaves, and another older shoot has six leaves in the whorl, while the latter number is also seen in another slide (S 2263). It is probable that the number varied in different plants of the same species between certain limits, while it probably increased with the relative size of the shoot.

The length of the leaves appears to have been from 1·5 to 2·5 mm., but perfectly median longitudinal sections are rare, and some may have been a little longer. Their breadth scarcely exceeds 0·8 mm. in the widest part, and they were about 0·5 mm. thick in the same region. In transverse section they present a somewhat semicircular outline, the outer side being convex and the adaxial side more or less flattened. The outline of the sections differs considerably, depending on the position in which they are cut. The centre of the adaxial side is often occupied by a ridge, usually with a slight groove at either side (*cf.* Plate 4, figs. 1 and 10). Towards the apex of the leaf the outline approaches a circular form (*cf.* Plate 3, fig. 1 ; Plate 4, fig. 1). In cases where the tissues are badly preserved and have shrunk the grooved shape of the inner side becomes more noticeable (*cf.* Plate 5, fig. 8). The

more or less triangular shapes described by HICK are due entirely to bad preservation. Longitudinal sections show that the leaves are linear and falcate, tapering to a point at the apex (Plate 3, fig. 7; Plate 4, fig. 12).

In describing the structure of the leaves it will be convenient to deal separately with each of the constituent tissues.

The Epidermis.

In the best preserved specimens this forms a very noticeable feature (*cf.* Plate 4, figs. 1, 9, and 10). When seen in transverse section, it consists of a layer of rather large cells with a rounded lumen. Longitudinal and tangential sections show that the cells are very much elongated in a direction parallel to the length of the leaf (*cf.* Plate 3, fig. 1). In most cases there is a well marked cuticle and the outer surface is quite smooth. There is a considerable difference between the cells composing the outer convex and the inner adaxial surface. The cells of the former are usually much larger than those of the latter region, and the cuticle is very much thicker. In some cases its thickness may exceed one-third that of the epidermal layer (*cf.* Plate 4, figs. 1, 9, and 10, text-figs. 4, 5). A few leaves, however, have been found in which the cuticle is thin all round the leaf and the surface slightly corrugated. The inner and radial walls of the epidermis are not specially thick. The lumina of the cells appear as though they were devoid of dense contents during life, but in a few cases (C 13) cells are filled with a dense brown substance, probably representing contents of some kind, possibly of the nature of tannin or mucilage or protoplasm. There are no stomata on the convex outer surface of the leaves; they occur only on the adaxial surface.

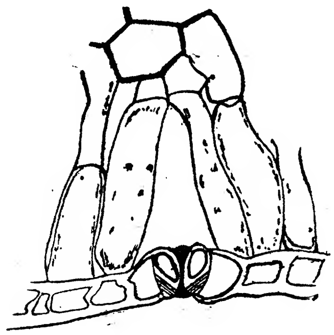
The Stomata.

This appears to be the first time that Calamite stomata have been fully described. Prof. SEWARD figured a section showing one, but it appears to have been badly preserved and little can be made out as to its structure. It may be interesting to recall here a paragraph from Sir J. D. HOOKER'S "Essay on the Vegetation of the Carboniferous Period as Compared with that of the Present Day," published in 1848. He says under the Calamiteæ, "I have in vain sought for any traces of structure in carefully prepared species of this genus, or for evidence of their being Equisetaceæ in the presence of those siliceous stomata with which that order abounds and which would surely have been preserved in the fossil state."* It is curious to notice that although it was anticipated that these organs would be among the earliest to be found, yet they were probably the only essential parts of the Calamite plant undescribed at the time this paper was commenced. From the subsequent description

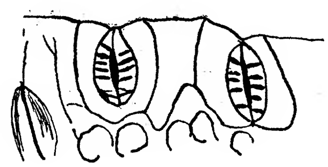
* HOOKER ('48), p. 427.

it will be seen that these stomata actually exhibit the characteristic structure seen in modern Equisetums.

The stomata are only seen in the best preserved specimens and are very small, the largest measuring about 0·03 × 0·02 mm. They seem to have been produced in lines with the pores parallel to the long axis of the leaf and were fairly close together. Their number appears to vary somewhat, in some transverse sections (Q 233) about eight to ten are seen, while in others only four or five can be distinguished (F 1). There is a tendency for the stomata to be absent from the central ridge of the adaxial surface.



TEXT-FIG. 2.—Section through one of the well-preserved Stomata seen in a Leaf in Slide F 1. The guard-cells, thickened on the upper side and surrounded by large epidermal cells, are shown. Below the stomata is a large air-space with palisade cells in either side. × 550.



TEXT-FIG. 3.—Drawing of the Stomata seen in Surface-View in Slide Q 233. The striated guard-cells and large epidermal cells are shown. These stomata are much larger than that seen in fig. 2. × 380.

In one section (H 2) showing part of the surface of the epidermis 16 stomata are seen, occupying a space of about 0·036 sq. mm. This gives the frequency of stomata at about 440 per sq. mm. The guard-cells of these average about 0·024 mm. long by 0·018 mm. across.

When examined in surface-view (Q 223) we find that they consist of two guard-cells, which are usually dark brown in colour (Plate 4, fig. 5, text-fig. 3). These are united at the ends in the usual way, and together present a rather elongated elliptical shape, the opening being seen as a dark line in the centre. It is interesting to note that the guard-cells are transversely striated, apparently with bands of thickening material. A similar thickening is characteristic of the stomata of all modern Equisetums, and this feature provides another interesting comparison between the structure of the plants of the two groups. The guard-cells are surrounded by a rounded clear epidermal cell, the usual shape of the epidermal cells being lost when the stomata are grouped together. In transverse sections through the leaves the stomata are often seen cut through, but owing to their small size it is very difficult to make out their exact structure. Usually they are level with the surface of the epidermis, but may be very slightly sunk in it (Plate 4, fig. 9). The guard-cells have a semicircular or in some cases slightly pear-shaped section

(Plate 4, fig. 9, text-fig. 2). The wall abutting on the opening is straight and almost as long as the cell, while the upper portion usually shows a dark band, probably of thickening material. The lower part of the cell is lighter in colour, but it is usually difficult to make out the shape of the lumen. On either side the auxiliary epidermal cells are seen, usually they are slightly enlarged and with a semilunar shape. On one of the flatter leaves described by HICK there is a very good transverse section of a stoma (Plate 4, figs. 10, 9), on the study of which most of these observations are based.

The Assimilating Tissue.

Below the epidermis there is a broad zone of thin-walled tissue which may be closely compared with the palisade layer of modern foliage leaves. In this species it forms a continuous cylinder round the central conducting tissue, but becomes narrower or disappears on the inner side toward the apex of the leaf. The structure of the leaf is, however, typically concentric. The assimilating tissue consists almost entirely of filament-like cells stretching straight across from the conducting cylinder to the epidermis. Almost all the cells appear to be separated by large air spaces, and transverse communicating cells are typically absent (see Plate 4, fig. 4). The arrangement of the cells is well brought out in badly preserved specimens (Plate 5, fig. 8) in which each cell has shrunk and assumed the appearance of a single radial cell wall when viewed in transverse section.

The size of the air spaces is best seen in tangential section (Plate 3, fig. 1; Plate 4, fig. 4). From the figures it will be seen that the palisade cells resemble a number of pillars supporting the epidermis, and standing up in the large air space into which the stomata open. The analogy can be carried further, for many of the cells are enlarged where they abut on the melasmatic tissue. The pillar may consist of a single cell or two or three filamentous cells joined end on end (*cf.* text-fig. 13, Plate 4, figs. 1, 9, and 10).

The cells are very thin-walled, and are usually clear and almost colourless. They occasionally contain one or two dark round spots which Prof. SEWARD has suggested* may represent mineralised nuclei, but the fact that cells often contain two or three of these dark bodies indicates that this hypothesis cannot be upheld. It is probably safer to regard them as the remains of cell-contents. In other cases some cells may have a deep brown colour, while they may often be partly or wholly filled with a mass of small round granules (Plate 4, figs. 6, 10), which seem to be connected only with the conditions of preservation, and probably have no important significance, for they occur very largely in badly preserved specimens. The expanded ends of the palisade cells usually abut directly on the peculiar sheath of cells which surrounds the bundle, and this must be next considered.

* SEWARD ('98).

The Bundle Sheath (*Melasmatic Tissue*).

In transverse sections we see a group of large cells round the vascular bundle, often with rather thicker walls. They are not very sharply marked off from the tissue of which the bundle is composed, but are characterised by the presence of a dense black mass in the centre of most of them (see Plate 4, figs. 1, 6, 9, 10; Plate 5, figs. 2, 3; text-figs. 4–12). In longitudinal sections they are seen to be elongated parenchyma often with rounded ends, and easily distinguished from the longer and narrow cells internal to them (Plate 3, figs. 1, 7; Plate 4, fig. 6; text-fig. 13). The thickness of their walls appears to vary with the conditions of preservation, and the appearance of the contents also differs considerably in different specimens. In some cases (text-fig. 13) the whole cell is filled by a light brown substance, in others it is dark brown or black. Usually, however, the contents are contracted to a black irregular mass in the centre, roughly of the same shape as the cell. Occasionally a fine membrane-like line can be seen surrounding the mass (Q 167), and in others there is a suggestion of threads connecting it to the walls (C 14, R 14). The cells form a continuous cylinder running up the leaf, though like the palisade tissue they may be absent on the adaxial side at the apex. Below, they appear to be sometimes continued into the cortex of the stem, where their occurrence has already been noted.

Hick seems to have been the first to notice this tissue, which he also found in the bracts of Calamostachys* and in young Calamite stems.† He considered that it was, morphologically, part of the mesophyll of the leaf, and gave it the name of "Melasmatic Tissue." It will be convenient to retain this term, for though the tissue may not be morphologically distinct yet it seems well defined physiologically. Its function will be considered later (p. 78).

The Vascular Bundle.

The vascular bundle is situated in the centre of the leaf. It is circular in transverse section, and is clearly divisible into two parts, a small group of tracheides more or less centrally placed, and a surrounding layer of thin-walled cells (see Plate 4, figs. 1, 10, text-figs. 4, 5). The xylem tracheides (or vessels) can easily be distinguished by their thicker walls when seen in transverse section. Their number varies from five to ten or twelve. In longitudinal section they are seen to have fine annular (or possibly spiral) thickenings which are well seen in Plate 4, fig. 6. A very similar type of vessel is seen in the leaf-sheaths of some modern Equisetums. The chief feature of interest with regard to the xylem is its very small size.

The thin-walled tissue surrounding the tracheides is of some interest, but it is

* Hick ('93).
† Hick ('94).

difficult to determine its nature. It is composed of elongated cells with very thin walls (*cf.* Plate 4, fig. 6), and the end walls are sometimes oblique. There is some variation in size, the outer cells being larger, but nothing of the nature of sieve-plates can be made out. The cells often contain dark spots, probably the remains of some kind of cell contents (S 900, Q 168, 169) (Plate 4, fig. 6.). There is nothing to show that any of these cells can strictly be designated phloem, though from their shape and construction they very probably acted as conducting parenchyma. When we consider that they are almost or completely absent in several other types of Calamocladus, it would seem that their function was not very important for the leaf. The tissue differs somewhat in appearance from the phloem of mature Calamite stems.

HICK and others have thought that the bundle was co-lateral in structure, but there seems to be no evidence for this statement. In some sections it is true that the xylem is not central, and lies nearer the abaxial side of the leaf (*cf.* Plate 4, fig. 1, *x*), but in others it lies nearer the opposite side. Since it is not possible to distinguish true phloem in the bundle we cannot say whether the latter is collateral or not, but if all the thin-walled tissue is taken to represent phloem the bundle must be considered to be concentric.

Its structure agrees very closely with that in the lower portion of the bracts of the cone *Calamostachys grandis*, Zeiller, which I have previously described.*

Mechanical Tissue.

Towards the upper portion of the leaf on the adaxial side of the bundle we often find some thickened elongated cells. Their number varies in different specimens, and also with the plane in which the section is cut. Near the middle of the leaf three or four cells, differentiated off from the bundle-sheath and the tissue near it, can be noticed (Plate 4, figs. 1, 10, text-figs. 4, 5). These increase in number towards the apex, and may there replace the palisade tissue on the adaxial side, forming a wedge-shaped group of cells (Plate 3, fig. 1, *t*). In longitudinal section they are seen to be elongated sclerenchymatous fibres (*cf.* Plate 4, fig. 6).

It is difficult to estimate their morphological nature. In some cases they seem to be derived from cells of the bundle-sheath and mesophyll, but in others they might be taken to be bast fibres, for towards the tip of the leaf they replace part of the conducting parenchyma of the bundle, and approach the xylem. No doubt they serve to impart rigidity to the leaf, which is otherwise an extremely delicate structure. It must be noted that in this species the number of fibres is always very small compared with that in leaves subsequently described.

* THOMAS ('09), p. 251.

Identification with Impression-Species.

The chief characteristics of the external form of the twigs of this type are : (*a*) the number (usually four) of leaves in the whorl ; (*b*) the small size and falcate shape of the leaves ; (*c*) their erect arrangement on the stem. When we examine the impression-species of Calamocladus found in the English Coal Measures, we find that these characters are also presented by *C. charæformis* (Sternb.) (= *Asterophyllites Rœhli*, Stur.). A specimen of this species in the Sedgwick Museum, Cambridge,* from the Middle Coal Measures of Barnsley, is shown in Plate 4, fig. 2. The ultimate branches are long and slender, about 0·7 mm. in diameter, bearing whorls about 1 mm. apart. Each whorl consists of about 4–6 small falcate leaves 1–2 mm. long. The leaves of successive whorls alternate in position on the stem, and they overlap slightly. The terminal bud is of simple structure, with only one or two whorls of sheathing leaves. This species differs in form from all the others, and there seems to be little doubt that it is identical with the petrified type. The chief difficulty to this hypothesis is the fact that, hitherto, impressions of *C. charæformis* have not been found lower than the Middle Coal Measures,† whereas it appears to be the commonest form in the calcareous nodules of the Lower Measures. Possibly it has escaped observation in the shales of the latter horizon, owing to its small size; while its delicate structure would probably increase the rarity of well-preserved specimens.

CHARÆFORMIS TYPE—VARIETY *a*.

The specimens examined show considerable variety in shape (*cf.* Plate 4, figs. 1, 3, 10). Slide No. Q 169 contains some very good longitudinal and transverse sections of leaves, which can in general be placed in the Charæformis section, but vary somewhat in structure also from the typical examples (*cf.* Plate 4, fig. 3, text-fig. 6). The vascular bundle is well preserved, consisting of four or five annular tracheides, surrounded by a well-marked layer of thin-walled elongated cells, which form a conspicuous feature in the leaf (see Plate 4, figs. 3, 6). The melasmatic tissue almost completely surrounds the bundle, forming a ring two or three cells broad ; it is interrupted on the adaxial side by a group of sclerenchymatous fibres. The latter, which arise a short way from the base of the leaf, increase to a broad strand towards the apex, where they form the tip of the leaf. The palisade tissue is considerably smaller in amount than in the other leaves of this type, the cells being shorter and more compact. One of the longitudinal sections of these leaves is very fine; it is shown in Plate 4, fig. 6. These leaves provide a transition stage in structure between the Charæformis type and the Grandis type. They resemble the former in their vascular bundle with conspicuous conducting parenchyma, and in having an

* No. 455 Carbon, Plant Collection.

† Dr. KIDSTON ('94) attributes it to the Upper Transition and Middle Coal Measures.

almost concentric structure near the base. They resemble the latter in the presence of a conspicuous strand of fibres—though much smaller, and a reduced amount of palisade tissue.

CHARÆFORMIS TYPE—VARIETY β.

Another slide from the Cash Collection (Q 167) at Manchester exhibits a structure again differing slightly from the others, and still further resembling *C. grandis*. Some of the leaves are very well preserved, and are seen cut through near the centre and near the tip. Part of the epidermis is perfect, the cells of the outer portion being very large (*cf.* Plate 5, figs. 10, 11). The cells of the assimilating tissue are closely approximated, and the intercellular spaces are considerably reduced. The vascular bundle presents the chief point of interest (see text-fig. 7). It consists of a small group of thin-walled cells with rather rectangular outlines, among which four or five small tracheides are found. The latter are not grouped together as in the cases previously described, but are more or less separated by parenchymatous cells, as shown in the figure. The whole bundle is smaller than in the normal Charæformis leaves, and shows an approach to that found in the Grandis type. The xylem increases in amount, and becomes more compact towards the tip of the leaf. The melasmatic tissue forms a crescentic group of cells round the bundle, and on the adaxial side there is a conspicuous strand of thick-walled fibres, twenty to thirty being seen in transverse section. The leaf, at first elliptical, becomes rather triangular in section near the tip (*cf.* Plate 5, fig. 11), but in this region its shape differs considerably from that seen in the Grandis type. The apex appears to consist of fibrous cells only.

TYPE II (*C. grandis*, STERNB.).

A second type of leaf can easily be distinguished from that previously described. Although almost the same tissues are present in both cases, yet they are present in very different proportions, and the general aspects of the cross-sections consequently present a noticeable difference (*cf.* text-figs. 8 and 5). This is chiefly due to the strong development of thick-walled fibres and the reduction of the vascular bundle in the species now to be described.

I have found a number of small linear leaves which can be compared with those known from impressions as *C. grandis* (Sternb.). They are longer than those of the Charæformis type, but rather similar in shape. I have previously figured and briefly described some of them, which I found in connection with a cone of the *Calamostachys Binneyana* type.*

No slides have yet been obtained showing transverse sections of stems clearly connected with these leaves; in several cases, however, stems and leaves have been found associated together in such a way as to make their original connection probable.

* THOMAS ('09).

Some longitudinal sections have also been found of stems with leaves of this type. The structure of the stem cannot be clearly made out from any of these, but it seems to have been slightly different from that of the Charæformis stem. The difference lies mainly in the xylem, which consisted of small groups of tracheides set in thick-walled ground tissue; the latter forms a great portion of the stele, and extends some distance inwards towards the centre. The carinal canals developed early, and are clearly distinguishable in a section only a little more than 1 mm. in diameter (Plate 3, fig. 8). These twigs resemble the young stems previously described* much more closely than do those of the Charæformis type.

The leaves had a length of 3–4 mm., and were about 0·75 mm. broad. In the absence of good transverse sections through a leafy shoot, it is not possible to determine the number which occurred in a whorl. However, in case of the shoot below the cone,† a tangential section showed parts of four leaves in some whorls, and the complete number was therefore probably near 10 or 12 in this example.

As seen in transverse section, the outline of the leaves does not differ greatly from that seen in the Charæformis type, but the structure is very different. About half of the leaf is composed of sclerenchymatous fibres, which occupy almost the whole of the adaxial side. The appearance varies considerably according as the leaf is cut through near the base or the apex. Near the base the tissue is less differentiated. The fibres are not yet strongly thickened, and there is little assimilating tissue. The vascular bundle was very inconspicuous, consisting of about eight very small tracheides with but little thin-walled or phloem tissue (now decayed), and surrounded by larger cells apparently belonging to the sclerenchyma. The melasmatic tissue with its dark contents is, however, already very noticeable.

Near the apex of the leaf the tissue is clearly divisible into two parts (see Plate 4, fig. 11), one, nearest the stem, consisting of an elliptical mass of thick-walled fibres, while the other half is composed of thin-walled mesophyll (usually badly preserved). The xylem is small in amount and slightly sunk in the fibres. A little thin-walled central tissue is present which merges into five or six larger cells of the melasmatic tissue lying between the xylem and mesophyll. A well-marked epidermis, with rather thickened cuticle, is seen to the outside of the mesophyll. It extends over part of the fibres, but it cannot be traced all round them. In sections cut closer to the apex the mesophyll is reduced to a still smaller patch, and probably was absent from the tip of the leaves.

Transverse sections cut through near the middle of the leaves show the following features (text-fig. 8 and Plate 4, fig. 7):—The sclerenchymatous fibres form a compact elliptical mass of tissue on the adaxial side. The bundle occupies the centre of the leaf, and though indistinct seems to consist of some 8–10 tracheides rather irregularly arranged, together with a few thin-walled cells. A layer of melasmatic

* Hick ('94), Williamson and Scott ('94), Scott ('08), p. 22, fig. 5.

† See above.

tissue, typically one cell thick and having the usual characters, extends round the bundle and fibres, separating them from the mesophyll. The latter forms a crescentic band on the abaxial side of the leaf, becoming enlarged into wing-like expansions at the sides. The palisade tissue is not so well developed as in the former type, the cells being shorter. It is also very much more compact, and the intercellular spaces are small when compared with those previously seen. The cells of the palisade tissue are often obliquely arranged. The epidermis forms a well-marked feature on the convex side, and has a fairly thick cuticle. On the flat side it is not so conspicuous, and cannot be distinguished on the outside of the fibres. Stomata are not very common in leaves of this type; several have been noticed, however, and they seem to agree in structure with those described above. No cases have been noticed where they occur on the convex surface, but they are chiefly found on the adaxial side of the wing-like expansions of the mesophyll. Longitudinal sections show few new points of interest. In Plate 4, fig. 7, the long fibres, much thickened in the upper part of the leaf, are seen. The xylem tracheides are very small; they are accompanied by one or two elongated cells, but nothing of the nature of sieve-tubes can be distinguished. The melasmatic tissue forms a very conspicuous feature, and the palisade cells are in contact with it.

The chief structural characters of these leaves are, then: (*a*) The presence of a large strand of sclerenchymatous tissue, elliptical in cross-section. (*b*) A very small vascular bundle, the usual elongated parenchyma being very much reduced, and perhaps absent in some cases. (*c*) Reduction in the intercellular spaces. (*d*) Palisade cells shorter, and often obliquely placed with reference to the epidermis.

I have referred these leaves to the species *Calamocladus grandis* (Sternb.). The latter is characterised by M. ZEILLER as follows:—"Ramules longs de 2–8 cm., à articles longs de 2–4 mm., larges de $\frac{1}{2}$–1 mm. et très finement striés en long. Feuilles linéaires et presque filiformes, effilées en point, étalées ou légèrement dressées à leur base et courbées en crochet vers le haut, longues de 3–8 mm. empiétant à peine d'un article sur le suivant, uninerviées, au nombre de 8–10 par verticelle."*

The description would seem to apply without qualification to the petrified species. The strand of fibres, being the toughest part of the leaf, had evidently left its trace in the impression and had given rise to the statement that the leaves were uninerved. Additional evidence is furnished from the fact that leaves of this type have been found attached to a Calamostachys cone in both impression and petrified examples. Impressions of *C. grandis* occur in the Middle and Lower Coal Measures.†

* ZEILLER ('86), p. 377.

† KIDSTON ('94).

Grandis Type—Variety α.

One of the sections containing the cone already described also shows another leafy twig. The leaves on and near it are of a variety rather different from the Grandis type (Plate 4, fig. 8, text-fig. 9). They are smaller (about 2 mm. long and 0·6 mm. broad), more flattened, and do not seem to have been falcate like the others. They are not well preserved, but the following features can be noticed :—The amount of sclerenchymatous tissues is smaller, and it does not form a ridge on the adaxial surface. The vascular bundle in the centre is very small and flattened ; little or no parenchymatous tissue is present in it. The melasmatic tissue forms a conspicuous band in the centre of the leaf. The palisade tissue is only preserved in a few places, but was considerable in amount ; it seems to have been of the same type as in *C. grandis*. The cells of the epidermis are large and the cuticle thick. The stomata, as usual, were produced on the adaxial side, and were probably slightly sunk ; a tangential section near the surface shows a number of them with but few portions of epidermal cells (Plate 5, fig. 7).

While closely resembling the species just described, these leaves show interesting variations. Though the bundle is of a kind very unlike that in the Charæformis leaf, the proportions of the fibres and mesophyll approach what is seen in the β variety of that type (*cf.* text-figs. 7 and 9). I think that it is not unlikely that these leaves belonged to the same plant which bore also typical Grandis leaves, and furnish a useful sample of the range of variation of these structures. At the same time, they show the transition stages, which are often found connecting up the different types.

Type III (Equisetiformis, Schl. ?).

The great majority of the petrified Calamite leaves hitherto found are very small, while several of the species of Calamocladus found in impressions have leaves of a considerable length.

I have, however, obtained four slides containing leaves which probably belonged to the larger types. Two of them are transverse sections, probably referable to the same species ; the others are longitudinal sections, which may, or may not, be related to the rest or to each other.

The most interesting specimen (A 89) is a transverse section passing through a bud, probably above the stem. Parts of seven or eight whorls of leaves are seen, arranged round each other in concentric circles (Plate 5, fig. 5). The section is unfortunately broken through on one side, and just below the fracture is seen part of another bud (b_2 in figure) with five or six whorls of leaves. The leaves of both buds show the same general characteristics.

In the larger bud the three whorls nearest the centre were in an embryonic condition (see p. 74). The fourth whorl is much further developed, though bad

preservation renders it impossible to make out the details of structure. The epidermis, palisade tissue, and melasmatic tissue were probably differentiated, but the fibres are just beginning to form (Plate 5, fig. 6, *a*). The leaves have a peculiar shape, the adaxial side is almost flat, and has broad wing-like expansions on each side, which touch or overlap those of the leaves on either side. I think it probable that the expansions mentioned might appear in impressions as tissue uniting together the leaves of a whorl near their base. The structure of the leaves in the next two whorls is very characteristic (*cf.* text-fig. 11), the most noticeable feature being a large circular strand of cells—probably sclerenchymatous—with very thick walls. This strand in the lower part of the leaves is almost surrounded by the mesophyll, but in the higher parts the latter gradually recedes from the adaxial side. Near the tip the mesophyll formed a small triangular patch on the abaxial side, while the apex consisted of the fibres alone. Some of the stages are indicated in figs. 5 and 6, Plate 5.

Apart from the fibres, the other tissues are badly preserved. The vascular bundle was extremely small and inconspicuous. A few cells, which may be xylem, are sometimes discoverable about the centre of the leaf on the abaxial side of the fibres, but in most of the transverse sections no bundle can be seen. There was certainly no conducting parenchyma of the type seen in *C. charæformis*. The melasmatic tissue consists of a well-marked group of ten or twelve large cells, with their characteristic contents, forming a semicircular band between the fibres and assimilating tissue. It is usually better developed towards the centre of the leaf than at the sides. The epidermis is usually present on the outer side, where it consists of large cells, with a moderately thick cuticle. On the inner side the epidermis is thinner. There is a groove between the fibres and the edge of the leaf; the stomata were probably situated in this, but none have yet been made out. The fully-developed leaves seem to have been about 0·5 mm. broad and 0·3 mm. thick. The whole bud had a diameter of about 3·5 mm. There are eight leaves in each of the two innermost whorls, further out the number increases to 10, and was probably 12 or more in the outermost whorls.

Another slide (Q 223) shows some transverse sections of leaves similar in structure. In these, however, a few xylem tracheides are seen in the centre of the leaf between the fibres and the melasmatic tissue. The mesophyll is fairly well preserved in parts, and seems to be of a compact nature, while a few remains of stomata are found in the grooves.

No complete longitudinal sections have been found which can be definitely recognised as belonging to this type. It is probable, however, that the leaves had a considerable length, because so many whorls (three of which are fully developed) are found in the bud section. The outer whorls are cut through quite transversely, showing that the leaves must have had an erect position on the stem. Buds resembling this one in the large number of whorls and the erect position of the leaves are found in impressions terminating most of the branchlets of *Calamocladus*

equisetiformis (Schl.). An example from the Forest of Dean is shown in Plate 5, fig. 4 ; it is much larger than the petrified specimen, but the size of these buds varies considerably. The leaves of the same species have been described by Zeiller thus :—" Feuilles linéaires, effilées en pointe aiguë, étalées-dressées ou plus rarement tout à fait étalées, d'ordinaire un peu arquées, empiétant d'un verticelle sur le suivant, longues 7–20 mm., larges de 0·25–1 mm., exactement contigues à la base, uninerviées, au nombre de 12 à 16 et peut-être 20 par verticelle" . . . . "elles montrent toujours nettement leur nervure unique, souvent assez large et limitée par deux lignes parallèles qui ont pu faire croire parfois à l'existence de deux nervures."*

Though in the absence of longitudinal sections it is impossible to be sure of the species of the petrified specimen, yet there are many indications in favour of *C. equisetiformis*, while there seems to be little evidence against it. The fibres, giving rise to a well-marked single nerve, and the stomatal grooves on either side are strong points of comparison.

The longer of the longitudinal sections of leaves may or may not belong to this type. Both of them are connected with fairly large stems, but since impressions show that the leaves increased in size with the age of the stem, they may really have been originated as foliage of the *C. grandis* type. In one specimen (A 64) the stem has a diameter of about 2·5 mm. It is cut in an oblique longitudinal direction, and shows the usual characters of a Calamite stem. The cortex is badly preserved, but the remains of leaves are seen on either side of a node. These are 6 and 7 mm. in length, and were obviously much larger when living. They are chiefly composed of sclerenchymatous fibres, but some remains of parenchymatous tissue, with a few melasmatic cells, are seen towards the basal end. This section is chiefly of interest, as showing the remains of leaves attached to a typical Calamite stem. Another leaf section (C 11) is about 7 mm. long. It is chiefly composed of fibres, with a well-marked strand of melasmatic tissue and some palisade cells. Towards the apex some xylem is seen, consisting of nine or ten tracheides, with the usual thickenings. There are indications in several specimens that the xylem increased in amount towards the apex of the leaf as it did here. This leaf was probably attached to a stem, which is seen near its base, and which has a structure similar to that mentioned in relation with *C. grandis*. It is quite probable that this was one of the older leaves of that type.

Type IV (Scotti).

Two slides have been obtained which show leaves of a type which can be distinguished without difficulty from all those previously described. They are characterised by a very small development of palisade tissue, while the melasmatic tissue is very conspicuous, and occupies a considerable portion of the leaf. One of the sections (S 2455) passes obliquely through a bud in a longitudinal tangential

* Zeiller ('86), pp. 369–370.

direction (see Plate 5, fig. 1). It cuts the upper leaves just above the stem, and shows eight leaves in a whorl in this position. The leaves are full of dense black carbonaceous substance, and are obviously rudimentary. Most of the lower leaves are cut through transversely, and their structure is well seen. These sections show a rather flattened elliptical shape, the edges being more rounded than in the other forms (see Plate 5, fig. 2, text-fig. 7). A wedge-shaped group of thick-walled sclerenchymatous fibres is found on the adaxial side. The point of the wedge is near the centre of the leaf, and immediately below it there are four very small xylem tracheides, which are only visible owing to the excellent preservation of the slide (see Plate 5, fig. 3, x). Separated from the fibres by a few large thin-walled cells, we have the melasmatic tissue. It forms a band of considerable dimensions, and the cells are of very varied size, some of them being very large. In almost every cell there is a mass of opaque substance of a very irregular shape; in section it appears sometimes rounded or triangular, sometimes rectangular or crescentic. It may lie in the centre or at one side near the wall, and is evidently not an original structure, but probably derived from the contents of the cells. Besides this, there is often a rounded pellicle of varying thickness lying near the cell wall (Plate 5, fig. 3). In many cases it is united with the wall, and gives it a greater thickness, but often suggests the protoplasmic lining of the cell. A rather similar thing is seen, however, in many of the fibres, and the tissue in question must probably therefore be regarded as the inner part of the cell-wall, which has shrunk away from the middle lamella. Little can be said as to the palisade tissue. It is very badly preserved, but the portions left suggest that it had a character similar to that of the other leaves. It was more abundant at the sides of the leaves than at the centre, but there was very little of it in comparison with the amount present in the species described above. The epidermis is also badly preserved; it probably had the usual characters, including a rather thick cuticle. It extended all round the leaf, and seems to have the same structure in all parts. No stomata have yet been distinguished.

In the same slide there is an oblique longitudinal section through a similar twig. Only a small portion of the axis is seen, but its structure cannot be made out. The longest section of a leaf measures about 3 mm., and the complete structures do not seem to have been much longer than this. The small xylem tracheides show the usual annular thickening very well.

A slide from the Hick Collection in the Manchester Museum (R 7) shows some leaves which seem to be identical with those just described. They lie around a rather badly preserved stem, from which a lateral shoot has just been given off. The structure of the stem cannot be clearly made out, but it seems to differ somewhat from the usual type. Some remains of a narrow ring of xylem are seen, while there is a considerable development of thin-walled cortical tissue. Many of the leaves are well preserved, and show similar characters to those in Dr. SCOTT's slide.

The number of leaves in a whorl was probably large (12–16), judging from the number seen round half the stem. The cells of the melasmatic tissue are completely filled with a clear brown substance, as seen in some other cases. In one place well-preserved palisade cells with large interspaces can be made out. One leaf shows some small dark structures at the side which were probably stomata, but they are not clearly seen.

The affinities of these leaves are very doubtful. While showing a structure comparable with that seen in Types II and III, it is nevertheless quite distinct. They would probably give rise to impressions resembling *C. grandis*, but I am unaware of any species with which they can be correlated. They do not seem to be comparable with *C. lycopodiodes* (ZEILLER). In both the slides examined young lateral shoots are seen to be associated with the main stem, and this will probably be a feature of importance in ultimately recognising the species. The name *Calamocladus Scotti* may be given to this type of leaf.

TYPE V.

I have found three slides in the Williamson Collection at the British Museum (Nos. 1003, 1010, 1020) which contain several sections of leaves. These do not agree in structure very closely with any of the other types, and may possibly have belonged to another species. It must be noticed, however, that only a few transverse sections of these leaves are yet known; it is not possible to tell exactly the plane in which they are cut, and hence it is quite probable that they are only a variety of one of the previous types. The sections are fairly well preserved, and their structure can easily be made out from the figure (text-fig. 12), which should be compared with the other drawings on the same page. The outline is almost circular and the leaf distinctly bilateral. Some of the mesophyll, with its large intercellular spaces, is preserved: the cells abut on the melasmatic tissue, which forms a crescentic band. In the centre of the leaf there is a cavity with some small cells, probably tracheides, and a few traces of thin-walled tissue which had probably decayed considerably before preservation. The adaxial side of the leaf is occupied by cells, polygonal in cross-section; they are thin-walled near the outside, but are very much thickened towards the centre. There can be little doubt that the latter were sclerenchymatous. The epidermal tissues are not well preserved. Other sections show that the amount of thick-walled fibres (?) increased considerably nearer the tips of the leaves.

This type is marked off by a number of characteristics which may be seen from the figures. If we may assume that the central cavity was formerly occupied by thin-walled tissue this provides an important point of contrast with all the types save the first (Charæformis). The present leaves differ very much from that species in the disposition of their assimilating tissue and in the marked development of thick-walled fibrous elements (for it seems probable that the section figured was not cut

very near the tip of the leaf). A development of thin-walled cells on the *adaxial* side of the fibres, as seen in this case, is only found in other sections which are cut quite near the leaf base.

There is some justification for the supposition that this specimen belonged to another distinct species. It may be suggested that the leaves were of the long narrow type, possibly resembling *C. longifolius* (Sternb.).

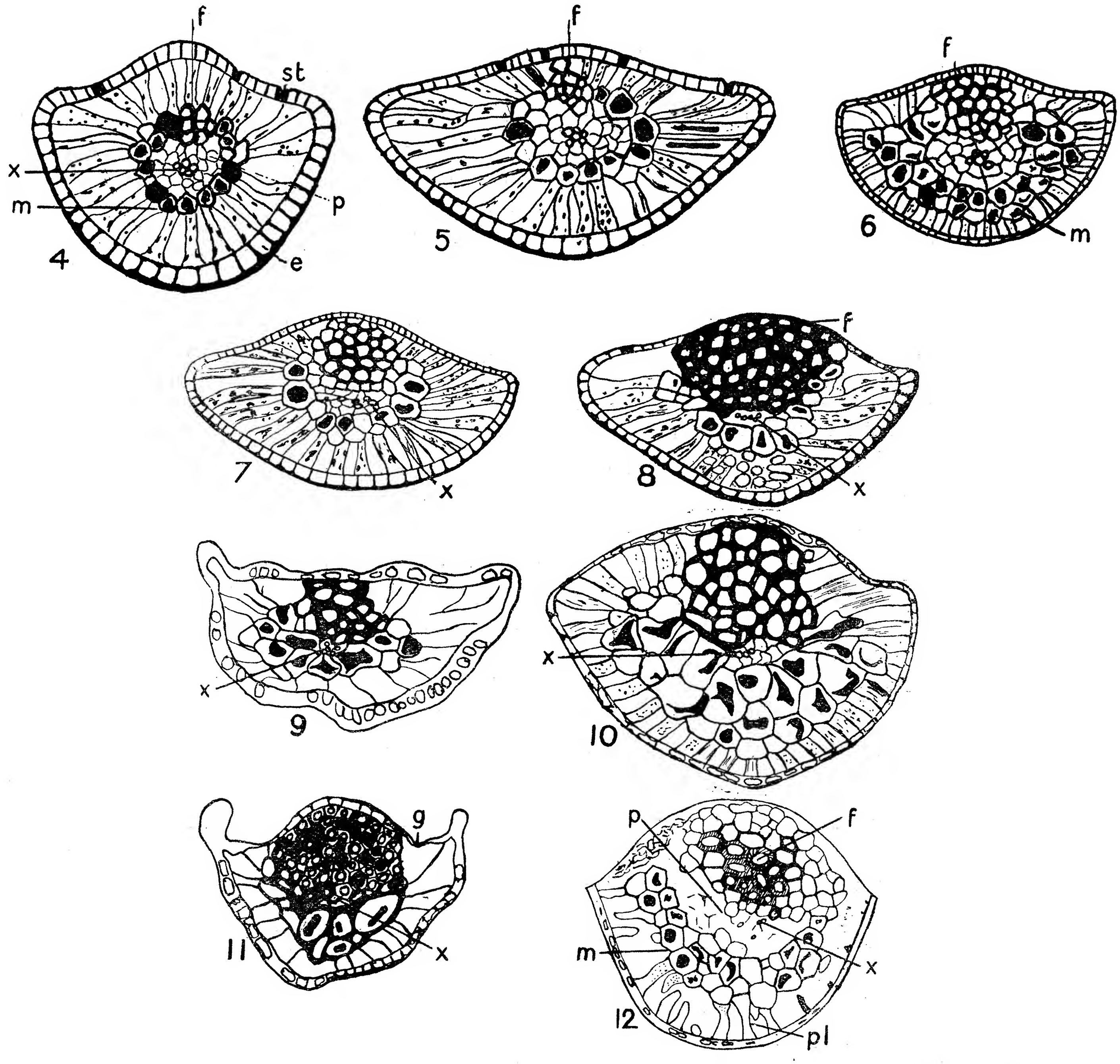
Terminal Buds and the Development of the Leaves.

Several of the sections show terminal buds at the apex of the twigs, and these present some points of interest. Sometimes the apical portion has become black and opaque, but in a few of the better preserved slides some of the structure can be made out. The arrangement and development of the leaves seems to differ slightly with the species.

Five longitudinal sections of buds have been found which appear to belong to the Charæformis type of plant (C 1, 2, 9, H 2, Q 233). The apex of the stem is a small rounded structure, but the details of its structure and the mode of origin of the leaves are not very clear. The cells round its periphery seem to be rather regularly arranged—as though they had recently divided, and usually contain dark contents. The central cells are much larger and rather irregular in shape. The apical cell is not clearly seen, as none of my sections are quite median. The apex is surrounded by the leaves of the first or second whorl, which bend over above it (*cf.* Plate 5, fig. 9). The leaves arise at a short distance from the tip, and are seen as masses of thin-walled tissue. They seem to grow rapidly, and are almost completely differentiated before the next leaves form, thus (as shown in the figure) the size and organisation of the two highest whorls are usually very different from the lower ones. The xylem and melasmatic tissue appear first in the leaf, and the palisade tissue is soon afterwards developed. The first few internodes are very short, the leaves almost touching, but the third is very much longer, and below this the shoot assumes its normal aspect.

In some of the other species the bud contains four or more undeveloped whorls of leaves. In Type IV the early structure is not well seen, all the cells being filled with dense black contents. In the third or fourth whorl from the apex the xylem becomes differentiated, and is clearly seen in the centre of the leaf. The epidermis is also developed early. In the fourth and fifth whorls the fibres are clearly seen, but are not yet strongly thickened. They appear first towards the tip of the leaf, being absent from the base. The palisade tissue seems to have been also present in this whorl. Probably the leaf was not fully developed till the sixth whorl.

A very similar structure is found in the Equisetiformis type. The three highest whorls of leaves are rudimentary and consist of cells with dense black contents. Little can be made out as to their structure, but the outline of the leaves in the third



TEXT-FIGS. 4–12.—Camera Lucida Drawings of Transverse Sections of the Various Types and Varieties of Leaves, all × about 100. Fig. 4, Type I, F 1. Fig. 5, Type I, a broader form, R 14. Fig, 6, Type I, Variety α, Q 169. Fig. 7, Type I, Variety β, Q 167, shows peculiar bundle and large strand of fibres. Fig. 8, Type II, C 5; the thick-walled fibrous elements and small bundle are noticeable features. Fig. 9, C 7, Type II, Variety α. Fig. 10, Type IV, S 2455. Fig. 11, Type III, A 89; the fibres and minute vascular bundle are noticeable. Fig. 12, Type V, section from the British Museum.

x = xylem; p = phloem (?); m = bundle sheath; f = fibres.

whorl shows an approach to the mature type. The fourth whorl is clearer; the edges now show wing-like expansions, and the xylem, some mesophyll, and a few fibres are seen, while the epidermis seems also to have been differentiated. The next whorl shows fully developed leaves. It must be noted, however, that in this specimen the members of successive whorls are not rigidly comparable because they are cut through at slightly different levels. The specimen nevertheless indicates quite accurately the general type of leaf development, which is similar to that of the leaves of Type IV. In these cases the black cell-contents in the young leaves closely resemble the contents of the melasmatic cells, and would probably be produced in a similar manner.

General Characters of the Calamite Leaves.

From the preceding description and the examination of the figures it will be seen that the leaves form a very definite group, agreeing for the most part in the possession of the same kind of tissues. The differences which exist between them are rather of degree than of kind, as would be anticipated, and the recognition of different species from structural characters is a task of considerable difficulty. As indicated above, there exist numerous specimens showing characters intermediate between those of forms which, taken by themselves, are quite distinct. At the same time a section taken near the tip of a leaf of one type often shows many features in common with a section through the centre of another type. In the present paper I have endeavoured to point out the chief variations in structure,* and there can be little doubt that these are accompanied by variations in the form and arrangement of the leaves. It is on the latter characters that the specific determinations of impressions are based, and the anatomical evidence seems to be quite in favour of the retention of these species. This, however, applies only to small specimens of the leafy terminal branches. It is, however, possible that leaves of different types were really produced on the same species of plant, and that the differences were due either to the position or age of the leafy twig or to the physical conditions of growth. Beyond the fact that the leaves on thicker stems were always larger and more numerous there is little evidence on this point. The question can only be settled by the collection and examination of a great number of larger and more complete specimens than those which we have hitherto had at our disposal. It is quite possible, too, that the leaves on the stems bearing cones had a slightly different structure from the young foliage leaves, but here, again, many more specimens are needed.

Turning now to other aspects of the subject, we see that, as a rule, the development of sclerenchymatous fibres corresponds with the length of the leaf. In the shorter species (*cf.* Charæformis) the fibres are only conspicuous near the apex, but in the longer ones a strand of fibres runs through the whole length. Again, among

* These can readily be seen in text-figs. 4–12, p. 75.

the larger forms the proportion of fibres seems to increase with the length of the leaf. This is a character often found among xerophytic plants, but here no doubt it was partly, if not wholly, due to mechanical considerations. In most cases also the amount of mesophyll seen in cross-section varies with the length of the leaf. We usually see much more in the smaller leaves, and in spite of the increase in size of many of them, the total volume of mesophyll may have remained about the same.

It is in all cases a very noticeable feature that the epidermis and cuticle are much thinner on the adaxial than on the other side, while at the same time the stomata are almost, if not entirely, confined to this surface. It is highly probable therefore that the inner (adaxial) side of the leaf was more protected than the outer from conditions likely to produce excessive evaporation. When the leaves are closely approximated to the stem, the protection may be effected by it, but in the examples studied this is seldom the case. A much more probable explanation is that the slender leafy twigs hung down from the tree in a pendulous fashion, so that the adaxial side of the leaf was also the under side. It is very common, particularly among tropical plants in great insolation, for the stomata to be produced only on the under side of the leaf, and for the cuticle to be much thicker on the exposed upper surface.* In this way excessive transpiration is checked, and at the same time the stomatal openings are not liable to become blocked by rain or dew. The theory that the twigs were pendulous is also supported by the delicate structure of the small stems, which possess little xylem to impart rigidity to them. [If this were the case, it seems likely that the cones also were borne in a similar manner. HICKLING's researches on Palæostachya† lend support to this, with evidence derived from another line of enquiry. He found that the condition of affairs in Palæostachya, where the sporangiophores are produced in the axils of the bracts beneath them, must be considered as secondary, and that the Calamostachys type of structure is more primitive. If the cones grew in an erect position there is no obvious reason for the production of the Palæostachya type, but if they were pendulous the change would be of great importance in improving the protection of the sporangiophores. It seems a very plausible hypothesis that the Palæostachya type was produced in response to a greater need of protecting the sporangia, and that at least some of its cones also were pendulous.‡]

Another feature that is noticeable in all cases is the very small size of the xylem and often of the vascular bundle. Even in the larger leaves there are seldom more than six or seven tracheides, and these have a very small diameter. Possibly this fact indicates that the transpiration current was not large, but of course the leaves are very small in size.

* Many shade-loving tropical plants have pendulous leaves, which are afforded protection against too much transpiration or insolation by this means, *cf.* KEEBLE ('95).

† HICKLING ('08).

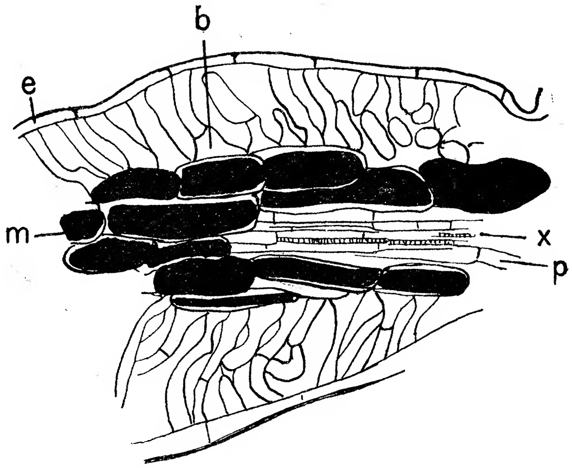
‡ It must be admitted, however, that some of the impressions of Palæostachya which have been figured do not support this view.

It may be pointed out here that all the cells in the leaves are small in size. It is sometimes remarked that fossil plants are characterised by the large size of their cells; but when we examine leaf structure we find that most of the cells and vessels are smaller than those in modern leaves.

It seems rather curious that we have not yet been able to recognise Annularian leaves in petrified material. I believe that this may be due to the fact they had an entirely different structure from the leaves of the Calamocladus group.

The Functions of the Melasmatic Tissue.

From the foregoing description it will be seen that a very definite and easily distinguishable group of cells, which, following Hick, I have called the melasmatic tissue, is present in all the leaves studied. In the isolateral leaves it almost forms a complete ring round the bundle, but in the dorsiventral types it usually forms a crescentic band between the mesophyll and vascular bundle. The appearance and structure of the tissue has been already described, and its physiological nature must now be considered.



Text-fig. 13.—Part of an Oblique Longitudinal Section of a Leaf of the Charæformis Type, Slide Q 168. The form of the epidermal cells and the palisade tissue are shown. The cells of the latter often show swollen ends (*b*) which abut on the melasmatic tissue. The structure of the bundle is also seen.

Some authors have suggested that its cell contents were derived from products of secretion,* but Hick thought it was comparable with the starch layer in the leaves of modern plants, on the grounds of its close association with the palisade tissue and vascular bundle. The present work strongly confirms the latter view. A considerable amount of the tissue is present in all the specimens, and this fact alone indicates that it had some vital importance. On one side the cells abut on the conducting parenchyma of the vascular bundle, while on the other they are in contact with the

* Scott ('08), p. 41.

ends of the palisade cells. The products of assimilation probably therefore passed through them. In some cases the ends of the palisade cells were enlarged at the point of contact with the dark cells (*cf.* text.-fig. 13, *b*), a method of connection between assimilating cells and bundle-sheath which is commonly found in modern plants. HABERLANDT* has figured the method of connection of the 'Zuleitungssystem' with the 'Ableitungssystem' in *Cycas circinalis*, which shows a structure that can be closely compared with that shown in my figure. An interesting comparison can be made between the nearly isolateral leaves of the Charæformis type and some of the figures of isolateral leaves given by HEINRICHER.† Their construction is strikingly similar in type, the palisade cells abutting directly on a sheath of cells surrounding the bundle. The leaves examined by HEINRICHER were taken from many different orders and genera, and it seems probable that this type of structure is fairly general (*cf.* HEINRICHER'S Plate 17, figs. 1, 2, 3, 5, 7; Plate 29, figs. 1 *b*, 2, 3, 4, of *Anchusa*, *Centaurea*, *Solidago*, *Scabiosa*, *Linum*, *Sarothamnus*). From the anatomy it seems impossible to escape the conclusion that the melasmatic tissue is the physiological equivalent of the bundle-sheath (*cf.* also HABERLANDT,‡ Plate 7, fig. 2; Plate 8, fig. 6).

It has been shown by these authors and others that the bundle-sheath is a tissue which is almost universally present in leaves. It was thought by SCHIMPER and others that it provided a path for the conduction of the products of assimilation. Mr. MANGHAM'S recent work,§ however, has shown that this view cannot be upheld, and while the bundle-sheath certainly does receive the assimilates, and may act as a reservoir for them, yet the actual conduction takes place chiefly in the phloem.

The relations of this tissue in the Calamite leaves favour the conclusion that here also the melasmatic tissue acted as a reservoir for assimilates. This tissue seems to be always present where assimilation was going on, thus it is also found in the free portion of the bracts of *Calamostachys Binneyana* (Carr), and also in the cortex of many young stems (which includes much thin-walled tissue, and may well have done some assimilation). Cells with similar contents have been observed in the leaves of other Carboniferous plants, and, though usually described as secretory, probably had the same functions as in the Calamites. In a modern plant we should expect to find the cells in such positions full of starch, and perhaps it was so in some of these ancient types. At the same time, it may be suggested that there is a possibility that the melasmatic tissue may also have taken some part in the conduction of the assimilates in some of these leaves. In the isolateral leaves elongated parenchymatous cells occur surrounding the xylem, which probably acted as conducting channels, though no typical phloem elements

* HABERLANDT ('82), fig. 15, Taf. VI.

† HEINRICHER ('84).

‡ HABERLANDT ('82).

§ MANGHAM ('11).

can be made out. But in the Grandis and Equisetiformis types there is little or none of this tissue, while a large amount of melasmatic tissue is present. Though in these cases the mesophyll is also rather reduced in amount, yet there is some justification for supposing that the melasmatic tissue may have replaced the phloem in the work of conducting assimilates. It may also be suggested that in several of the Palæozoic Pteridophytes the phloem may not yet have been a constant and well-defined tissue (as is the case in some Lepidodendrons).*

Some reference must be made to the nature of the black contents in the cells of this tissue. As has been mentioned above, they are sometimes light brown in colour and fill the cells entirely, and this, together with their irregular shape, would indicate that the black substance is the remains of the shrunken cell contents. These were probably different from the contents in the surrounding cells, though one can only conjecture what they were. The chief substances present must have been rich in carbon and insoluble in water. Starch would answer these requirements, though tannin is present in modern Equisetums, and also is often associated with assimilated food material. There seems to be no need to look upon the tissue as secretory. It does not seem possible to go beyond this until the nature of petrifaction is better understood.

Considerations as to Climate and Habitat.

It has been recognised for a long time that there is a definite relation between leaf-structure and the physical conditions of a plant's environment. The leaves of plants growing in a dry climate can, for the most part, be easily distinguished from those produced in a damp situation. Prof. Seward,† some time ago, drew attention to the possibility of determining ancient conditions of growth by the examination of leaf-structure, but little has been done in following out this line of enquiry. This, no doubt, is partly because so little is known of the details of Carboniferous leaf-structure.

There is now no need to refer to all the papers which have been written to show the effect of climate on leaf-structure. In the essay referred to above the results of Stahl, Haberlandt, Pick, Kerner and others are quoted by Professor Seward, and more recently the results of similar investigations have been summarised by Warming,‡ Clements,§ and others. Many interesting and useful accounts of the influence of different conditions on specific plants have also been published in ecological papers, of which those by Woodhead,|| Hesselman,¶ and

* Seward (99), ('02).
† Seward ('92), pp. 59–68.
‡ Warming ('09).
§ Clements ('05), Chapter III.
|| Woodhead ('06).
¶ Hesselman ('04).

HARSHBERGER* may be especially mentioned. Thus the relation between structure and habitat is well established for a large number of different conditions. To summarize briefly the main conclusions, we may say that leaf-structure is dependent on two main factors or stimuli, viz., moisture and light.† We have as yet no exact knowledge as to the effect of carbon dioxide on leaf structure.‡ In the case of most plants growing in ordinary conditions, it is extremely difficult to discriminate between the effect of decreased illumination and the effect of the decreased transpiration which is almost invariably associated with it.§ Most writers have simply studied sun and shade forms of leaves and have taken both the factors together. CLEMENTS, however, distinguishes several direct kinds of response due to the stimulus of light. The first is connected with the disposition of the chloroplasts; we cannot, however, expect to observe these in fossil plants. Then it would seem that the form of the mesophyll is directly affected by light. Palisade tissue is greater, and spongy tissue less, in amount in heliophylls than in sciophylls, and this does not appear to be entirely due to transpiration effects. The number of stomata is often much greater in sun leaves than shade leaves, and this character must be entirely independent of transpiration. Again, it is a fairly general fact that sun plants have shorter internodes than those growing in the shade, and stomata are very frequently confined to the lower face of the leaf.

The modifications due to water are more numerous and important. A water supply too small to come up to the requirements of transpiration operates on both the form and structure of leaves. A reduction of the transpiring surface may be brought about by decreasing the size and number of leaves, and linear or cylindrical leaves are very often produced in a dry situation. The position of the leaf may be changed. The production of hanging or erect leaves on many tropical trees is a device for reducing the intensity of insolation, and consequently the transpiration. Again, rolled leaves are typically xerophytic. With regard to structure, we find that the epidermis very frequently shows modifications. The thickening of the outer wall or cuticle almost invariably accompanies a dry situation, the cells of the epidermis become sometimes enlarged (consequent on greater need for water storage), and layers of hypodermal storage cells may also be present. WARMING

* HARSHBERGER ('09).

† CLEMENTS states that the normal stimuli of the plants of a formation are—"(1) water-content, (2) solutes, (3) humidity, (4) light, (5) temperature, (6) wind." But when leaves alone are considered, these can all be resolved into two, viz., moisture and light.

‡ FARMER and CHANDLER ('02) investigated the structure of several leaves grown by HORACE BROWN in an atmosphere rich in carbon dioxide. DEMOUSSY'S ('03, '04) subsequent work seems, however, to show that BROWN'S experiments were vitiated by acid impurities which checked the growth of the plant, and hence FARMER and CHANDLER'S results cannot be taken to represent the true effect of CO_2 on leaf structure.

§ WARMING ('09, p. 21) regards the regulation of transpiration as the most essential reason for the structural differences.

mentions that various substances produced in the epidermal cells may help to check transpiration; thus tannin is often present. The leaves in dry climates are often covered with a protecting coating of hairs or wax. The stomata may show well-marked xerophytic characters, being often reduced in number, sunk in cavities, or protected by the cuticle. With regard to the mesophyll, there may be a decrease in the size and number of air passages, and water-storage tissue may be developed. Some of the respiratory cavities may be cuticularised as well as the epidermis. Finally, the production of mechanical tissue seems to be a xerophytic character also. Numerous experiments have shown that mechanical tissue increases when transpiration is greater, and that it is more strongly developed in light than in darkness.* The decrease in water supply which seems to cause the above modifications may be brought about in many ways. The soil may be very dry, the humidity of the air very low, and evaporation great; transpiration may be greatly increased by the action of wind or by reason of a high temperature. On the other hand, the roots may be unable to absorb enough water owing to their feeble development, or because dissolved salts are present in excess in the soil water. There are then a considerable number of leaf characters which can be used to find out, within certain limits, the nature of the habitat in which a plant grows. We must now examine which of these characters are exhibited by the Calamite leaves. In the first place, the leaves are of the narrow and almost cylindrical type, so common among xerophytes. This feature, however, may be of a genetic nature, and not connected with an attempt to reduce transpiration. All the leaves seem to have hung down, and were so placed that the incident light struck them obliquely. The epidermis usually had a fairly thick cuticle, particularly on the upper and outer side; perhaps the epidermal cells sometimes possessed contents such as tannin or mucilage. The stomata were small, fairly numerous, and situated only on the protected side of the leaf. In one case they were slightly sunk. In the larger leaves there was a considerable development of mechanical tissue. All these are characters possessed by leaves growing in dry situations, but are usually more strongly developed than in the present specimens. On the other hand, the leaves described above possess several features which are distinctly hygrophytic. In the smaller leaves the air spaces were extremely large and the mesophyll very loose in character. It is impossible to imagine a leaf with mesophyll of this texture growing in any place where the atmosphere was not very humid. In some of the longer leaves, however, there is evidence that the mesophyll was much more compact. The stomata were for the most part level with the surface of the leaf, and never deeply sunk. In the smaller leaves there are no traces of epidermal coverings, such as wax or hairs, and in some examples the cuticle is thin all round the leaf. There is no water-storage tissue, and the xylem strands are exceedingly small.

When we consider all the leaves, we find both xerophytic and hygrophytic

* WARMING ('09), p. 129.

characters; in some of the smaller forms the latter seem to predominate, and the reverse is the case in some of the larger examples. Taking everything into account, it may probably be said that, on the whole, the leaves are slightly xerophytic.

It may be that the remarkable development of long thread-like palisade cells and the almost complete absence of the ordinary type of spongy mesophyll indicates that the plants were subject to a considerable degree of illumination. And the production of stomata on the "lower" side only may also favour this conclusion.

It has been suggested* that the Coal Measure plants may have flourished in extensive salt marshes. This view has been adopted by WATSON and STOPES,† who think that "groves of large trees with small herbs between them grew in flat swampy levels between the high ground and the sea, the water around the roots being salt or brackish, and helping to preserve the fragments which fell into the pools. Vegetation somewhat of this type is found in the tropics in the mangrove swamps fringing the coast in many places, while the more northernly marshes are usually devoid of trees."

It is generally agreed that the presence of salt in the soil inhibits the free absorption of water by the roots,‡ and the plants are almost invariably xeromorphic. Now one of the commonest structural peculiarities found in salt-marsh plants is the great reduction of their intercellular spaces. The leaves of a large number of plants growing in mangrove swamps and on English and North American salt marshes, whose structure has been examined, illustrate this fact.

In the case of *Acrostichum aureum*, however, there is a fairly well developed lacunar system in the mesophyll,§ though the plant flourishes at some distance from the sea, and there may be little actual salt in the soil. If it is the case, as seems probable, that the presence of salt in the soil brings about a reduction in the air spaces of the mesophyll, the evidence derived from the Calamites is not favourable to the salt-marsh-habitat theory, for, as has been shown, the lacunar system is often remarkably well developed.

From the evidence at present available, it seems to me that the Coal Measure plants whose petrified remains are found in the English coal probably grew under conditions approximating to those of the swamp forest. The Great Dismal Swamp region of the United States of America‖ is an example of a large area over which such conditions prevail. At the present time, however, I do not wish to make any generalisations on this subject, which will be dealt with after my investigations on the leaf structures of other Coal Measure plants have been completed.

* BINNEY (48). DARWIN, in letters published 1903, pp. 218–220. SEWARD and HILL ('00).

† WATSON and STOPES ('08).

‡ SCHIMPER ('98), WARMING ('09), HARSHBERGER ('09), p. 75.

§ THOMAS, E. N. ('05), p. 184, Plate IV, fig. 9.

‖ KEARNEY ('01), SHALER ('90).

Phylogenetic Considerations.

It was hoped that the present work would throw some light on the question of the primitive megaphylly or microphylly of the Equisetales, and on their relationship to the other members of the Pteridophyta, but the evidence is not very easy to interpret.

By some authors the Equisetales are regarded as typically microphyllous and allied to Lycopodiales,* but Lignier has more recently put forward the view that they are in reality reduced megaphyllous forms, and places them with the Sphenophyllales in the group Articulatæ,† and this view is regarded favourably by Dr. Scott.‡ Prof. Lignier's conclusions are based—

(*a*) On the almost universally admitted relationship of the Equisetales to the Sphenophyllales. The latter had whorls of leaves at the nodes, and do not show leaf-gaps in the stele; but the dichotomising nervation of their leaves, together with the structure of their cones, are considered to indicate Filicinean ancestry.

(*b*) On the assumption that the single leaves of some Calamites may represent the deeply-divided segments of large primitive leaves.

(*c*) On the structure of some Calamite cones, in which the bundles of the axis give off two vascular strands, each supplying a leaf (bract).

(*d*) On the evidence derived from the little-known fossil Pseudobornia (and Archæocalamites).

The present work provides some fresh information relative to several of these points.

In the first place, the relationship of the Calamites to the Sphenophyllums is perhaps further brought out in the structure of the young stems and twigs here described. The steles of the Sphenophyllums were almost invariably triarch, and it is now evident that the same was the case in some Calamites. The latter often had tetrarch steles, however, and this observation is in accord with the frequent observation of three and four vascular bundles in the cones of *Calamostachys Binneyana* by Mr. Hickling.§ Though in none of the young twigs has any centripetal wood been observed (and in the specimen figured on Plate 3, fig. 6, there appears to be no room for any), yet the fact that the xylem forms a solid mass at the nodes, while a solid pith is often present in the internodes, may be taken as further indications of the former existence of centripetal xylem. Both the above are, however, very slender bases for a Sphenophyllum affinity.

When we consider the leaves, we see at once that in type and structure they are typically microphyllous. Neither is there any suggestion of their having arisen in

* Jeffrey ('02), p. 143.

† Lignier ('03 and '08).

‡ Scott ('10).

§ Hickling ('10).

pairs, with vascular strands derived from a single stem bundle. It seems tolerably clear that each leaf is connected with one stem bundle, and, further, that any increase in the number of leaves in a whorl is accompanied by an increase in the number of bundles in the stem. The suggestion that each of the leaves represented two or more fused segments of an original bifurcated one would be perfectly gratuitous, nor has the view that the bifurcation cut the original bundle in two, and specialised a separate bundle for each segment, much to commend it.*

The question of leaf-gaps is less easy. In the youngest stages of the stem, the stele in the internodes seems separated up into bundles by gaps of thin-walled tissue, though near the nodes the xylem was solid. In older stems, however (*cf.* Plate 3, fig. 3), the xylem was almost continuous, even away from the node. Narrow medullary rays may usually be distinguished, but do not become conspicuous until a much later stage, and it is doubtful, therefore, whether they can be regarded as representing the leaf-gaps with which we are familiar in megaphyllous plants.†

Apart from the evidence afforded by the bifurcation of the bundles supplying the sterile bracts in the cones of the Calamostachys type, there seems to be little evidence which is directly afforded by the Calamites in favour of the theory of their Filicinean descent, and of their reduction from a megaphyllous form. The structure of the foliage shoots of Archæocalamites points in this direction, but, until we know more of this plant, the theory can be little more than a hypothesis.

SUMMARY.

1. A considerable number of leaves belonging to the genus Calamocladus have been found in petrified material, mostly derived from the Halifax Hard Bed (Lower Coal Measures), but no leaves referable to the section Annularia have yet been found.

2. On comparing their microscopic structure, five types of leaf can be distinguished, which are somewhat clearly marked off from each other, while three other examples are sufficiently distinct to be classed as varieties. Several of these types correspond with different species as known from impressions, but there is the possibility that two or more may be different growth forms from the same plant.

3. The most frequently occurring type is probably identical with the impression-species *C. charæformis.* The leaves are small falcate structures borne in alternating whorls of four on slender twigs. They possess a minute vascular bundle consisting of a few tracheides surrounded by thin-walled elongated cells. The bundle sheath or "melasmatic tissue" is well marked, its cells being filled with characteristic dense black contents. The palisade tissue surrounds the leaf, showing peculiar filament-like

* LIGNIER ('03).

† I am aware, however, that it may be argued with some justice that the present leaves are too small to have caused any appreciable leaf-gaps, and perhaps represent an extreme case of reduction.

cells with large interspaces. The epidermis usually has larger cells, with a thicker cuticle on the adaxial side of the leaf.

4. The stomata were produced on the adaxial side only, and were level with the surface. Their guard-cells are characterised by transverse striations such as are seen in recent Equisetums.

5. The twigs bearing these leaves have a structure somewhat different from that seen in the Calamite stems previously described. The youngest specimens show a solid stele with a pith, four groups of tracheides in the internodes, and a solid mass of tracheides at the nodes. In older specimens the pith tissue and xylem increase in size, and the former ultimately becomes disorganised in the centre, but carinal canals are only formed at a comparatively late period. Several points of comparison can be instituted between the structure of these twigs and that of young Equisetum stems described by JEFFREY.*

6. Two varieties of this type (Charæformis) have been noticed, which differ in the structure of their bundle and in the development of fibres on the adaxial side of the bundle.

7. A second type of leaf may be compared with *C. grandis*. It possesses a well-marked strand of thick-walled fibres on the adaxial side. The thin-walled tissue in the bundle is much reduced, and the palisade tissue is stouter and closer in texture.

8. A transverse section through a leaf bud shows a type of leaf differing from the above in the presence of a prominent circular patch of fibres and in the inconspicuous nature of the bundle, as well as in their general outline. These leaves may perhaps be identical with *C. equisetiformis.*

9. Another very distinct type is one in which the melasmatic tissue is very conspicuous, while the bundle is again very small. A wedge-shaped strand of fibres is present, and the outline of the sections is almost elliptical. This is considered to be a new species, *Calamocladus Scotti.*

10. A fifth type of leaf is founded on a few transverse sections in which the proportions of the tissues and their arrangement are different from the others, but nothing is known as to the length of these leaves and their affinities with impression-species.

11. The nature of the bundle-sheath or melasmatic tissue is discussed, and it is concluded that it probably functioned in the storage and possibly the conduction of the products of assimilation.

12. The general structure of the leaves in relation to the question of a probable habitat is discussed. The leafy twigs seem to have grown in a pendulous fashion, and the structure of the mesophyll and epidermis suggests that the habitat was a damp one. On the other hand, the leaves possess some xeromorphic features, such as the presence of fibres in the longer forms. The evidence points to a marsh or swamp forest as their habitat; this may have been near the sea, but if so the soil probably contained little salt.

* JEFFREY ('99).

13. In their structure and mode of origin the Calamŏcladus leaves appear to be typically microphyllous. No evidence has been obtained from this enquiry in favour of the view of the Filicinian origin of the Equisetales.

In conclusion, I should like to express my thanks to Mr. NEWELL ARBER, at whose suggestion the work was commenced, to Prof. SEWARD, for much helpful assistance and criticism, and to Dr. SCOTT for information and advice. Dr. BLACKMAN, Mr. MANGHAM, and other friends have kindly furnished me with information, and Prof. WEISS, Prof. F. W. OLIVER, and Mr. D. M. S. WATSON have lent me slides; to all these gentlemen I am deeply indebted.

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DESCRIPTION OF THE PLATES.

(Photographs by the Author.)

PLATE 3.

Fig. 1.—Slide R 945. Transverse section of leafy twig of Charæformis type, showing well-preserved stem with bases of two leaves. The solid xylem (*x*) with leaf traces is seen in the centre, surrounded by thin-walled phloem ? (*p*) and cortical tissue. Epidermis (*e*) and palisade tissue (*pl*) are well seen in the leaves. To the right is a section through the tip of a leaf belonging to the lower whorl (*t*). × 60.

Fig. 2.—Slide S 900. Transverse section through older stem showing stele which has a ring of xylem (*x*) with medullary rays (*r*). Thin-walled phloem tissue (*p*) surrounds it, while the cortical tissue is broad. Cells of the inner layer have dark contents (*m*). The epidermis is seen in one place (*e*), also a leaf trace (*lt*). × 60.

Fig. 3.—Slide H 1*b*. Transverse section of a similar stem. The xylem (*x*) has no carinal canals, but a pith in the centre. The other tissues are not clear. The stem is surrounded by sections of leaves (*ls*). × 60.

Fig. 4.—Slide R 945. Transverse section through larger stem, showing hollow pith, ring of xylem (*x*) with some medullary rays (*r*); inner cortical tissue with black contents in some cells (*m*); epidermis (*e*). × 24.

Fig. 5.—Section H 1*c*. Transverse section of young stem showing the carinal canal in process of formation. There is a considerable amount of xylem, separated into distinct bundles. In most of these there is a carinal canal (*cc*), but in at least two the protoxylem (*px*) seemed to be still intact. × 25.

Fig. 6.—Slide A 189. Transverse section through very young Calamite stem, showing triarch stele in centre. The three carinal canals can just be made out. The inner zone of cortical tissue is composed of cells with black contents (*m*). × 30.

Fig. 7.—Slide Q 167. Longitudinal section of leaf of β variety, Charæformis type, showing the relations of the fibres (*f*) and the palisade cells abutting on the melasmatic tissue. × 60.

Fig. 8.—Slide C 7. Transverse oblique section of stem, associated with leaves of the Grandis type. The xylem is split up into bundles, each having a carinal canal (*cc*). Several leaf bases (*lb*) are seen round the stem. × 60.

Plate 4.

Fig. 1.—Section F 1 shows two transverse sections through the upper portion of narrow leaves of the Charæformis type. The principal tissues can be made out. Epidermis (*e*) with cuticle, broader on the abaxial (more convex) side. Palisade tissue (*pl*), with large intercellular spaces. Bundle sheath or "melasmatic tissue" (*m*), with the vascular bundle inside, having the xylem (*x*) near the centre. The stomata (*st*) are not well preserved. A few fibres (*f*) are seen. × 60.

Fig. 2.—Photo of an impression of *C. charæformis* from the Middle Coal Measures of Barnsley. No. 455. Carbon Plant Collection, Sedgwick Museum. The shape and arrangement of the leaves and bud are seen. × 4·5.

Fig. 3.—Slide Q 169. Several transverse sections of leaves of the α variety of the Charæformis type. The conspicuous melasmatic tissue and reduced amount of palisade cells may be seen. *Cf.* with text-fig. 6. Lettering as before. × 30.

Fig. 4.—Section C 14. Tangential section through a leaf, showing the nature of the palisade tissue and the large intercellular spaces. × 60.

Fig. 5.—Section Q 233. Enlarged view of some stomata. The brown guard cells, with narrow slit, and the large auxiliary epidermal cells can be clearly seen; *cf.* also text-fig. 3. × 150.

Fig. 6.—Q 169. Portion of a longitudinal section of a leaf of the Charæformis α variety, highly magnified. The fibres (*f*), vascular bundle with annular xylem (*x*) and conducting parenchyma (*p*), are well seen. Below is part of the melasmatic tissue with characteristic contents (*m*) and a portion of the mesophyll (*pl*). The dark spots (*a*) probably are formed from cell-contents. × 170.

Fig. 7.—Slide C 5. Some of the leaf sections of the Grandis type, the principal tissues are seen in both transverse and longitudinal section. × 60.

Fig. 8.—Slide C 7. Transverse sections through leaves of variety α, Grandis type. The vascular bundle is very much reduced, and cannot be made out. The disposition of the fibres and melasmatic tissue is characteristic. $\times 60$.

Fig. 9.—Section R 14. Enlarged portion of leaf seen in fig. 10, to show the slightly sunken stomata (*st*). The lumina of the guard cells can just be made out, while the structure of the epidermis and palisade tissue is well illustrated. $\times 200$.

Fig. 10.—Section R 14. Fine transverse section of broad leaf of Charæformis type. All the tissues are seen. Outer epidermis (e_1) is noticeably thicker than the inner (e_2). Other lettering as in fig. 1. $\times 60$.

Fig. 11.—C 5. Tips of some of the leaves of the Grandis type, showing the characteristic arrangement of the fibres (*f*). $\times 60$.

Fig. 12.—Section C 13. Small longitudinal section through a leafy twig. The section is very thick and badly preserved, but shows the shape and arrangement of the leaves. The nodal swellings of the xylem can just be made out at (*n*). $\times 20$.

Plate 5.

Fig. 1.—Section S 2455. Fine oblique tangential section through a bud with leaves of Type IV. In the upper part the black undeveloped leaves of the apex are seen (*a*), and lower down the leaves are fully developed. At (*b*) another small bud is seen. $\times 14$.

Fig. 2.—Part of S 2455, showing several leaves. The characteristic shape of the latter, with the wedge-like strand of fibres (*f*), is well seen. The melasmatic tissue (*m*) with its large cells and their black contents are easily recognisable, but the palisade tissue and the epidermis are badly preserved. The tiny tracheides can be made out in the centre of several sections. $\times 60$.

Fig. 3.—Central portion of one of the same leaves more highly magnified. Four small tracheides (*x*) can be seen in the middle, together with a few larger thin-walled cells (*p*). Lying on one side of them are the fibrous cells, while on the other there is a characteristic portion of the melasmatic tissue. In both these tissues cells are seen (*a*) in which part of the wall seems to have contracted away from the middle lamella. $\times 180$.

Fig. 4.—Impression of a large bud of the Equisetiformis type from the Forest of Dean Coal Measures. No. 1719, Carbon Plant Collection, Sedgwick Museum. Slightly magnified.

Fig. 5.—Slide 89. Section through bud with leaves probably of the Equisetiformis type (Type III). A smaller side bud is seen at (*b*). The general form and arrangement of both the leaves and the bud can be made out. $\times 18$.

Fig. 6.—Part of the same more enlarged. Shows undeveloped leaves of the fourth whorl with sides overlapping (*a*). Fully developed leaves with their characteristic strand of fibres are seen at (*f*), and at (*t*) the fibrous tip of another leaf is visible. $\times 70$.

Fig. 7.—Slide C 7. Tangential longitudinal section through a leaf of the α variety of the Grandis type, showing fibres, melasmatic tissue, mesophyll, and some stomata. $\times 50$.

Fig. 8.—Section R 945. Transverse section through a group of leaves, which seem to have shrivelled up somewhat before preservation. Many specimens are found in this state. Two whorls are cut through, and the arrangement of the leaves in fours is well seen. $\times 32$.

Fig. 9.—Section H 2. Longitudinal section near the apex of a stem of the Charæformis type, showing the leaf bud. The actual apex of the stem is not clear, but the primordia of the first leaves are seen (*a*). The second whorl of leaves is very well developed; the xylem (*x*) of one of them is seen. The third whorl is closely approximated to the second. $\times 20$.

Fig. 10.—Slide Q 167. Transverse section through leaf of β variety, Charæformis type. The bundle is compressed and the xylem tracheides separated (*cf.* text-fig. 7). There are a number of fibrous cells, and the palisade tissue is compact. The difference between the inner and outer epidermis, where seen, is striking. $\times 60$.

Fig. 11.—Same, showing a leaf cut through near the tip. The arrangement of the fibres and other tissue can just be made out. $\times 60$.

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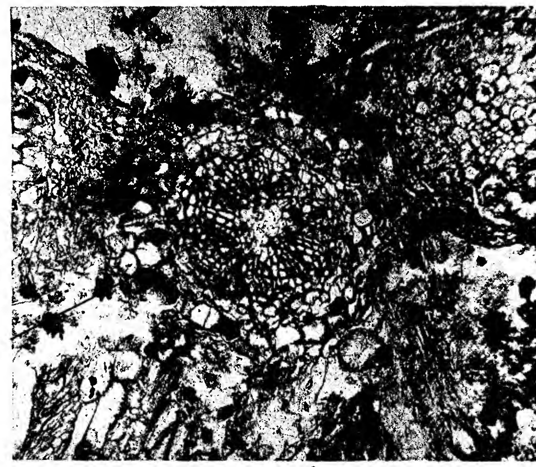

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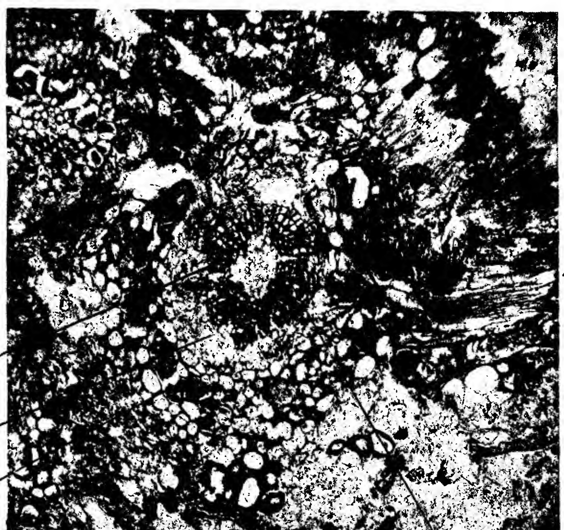

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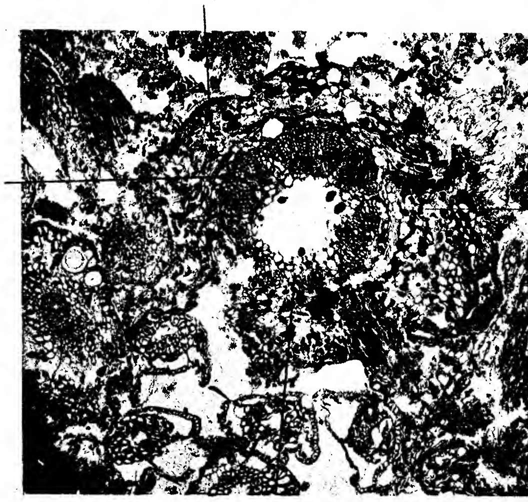

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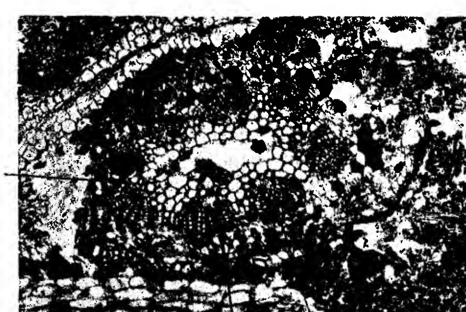

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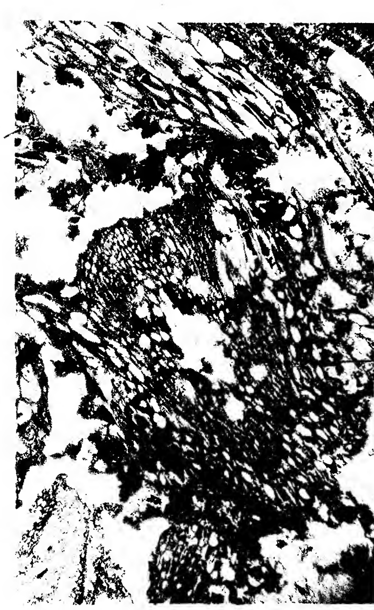

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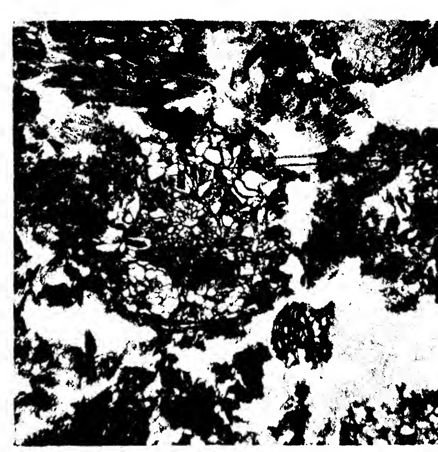

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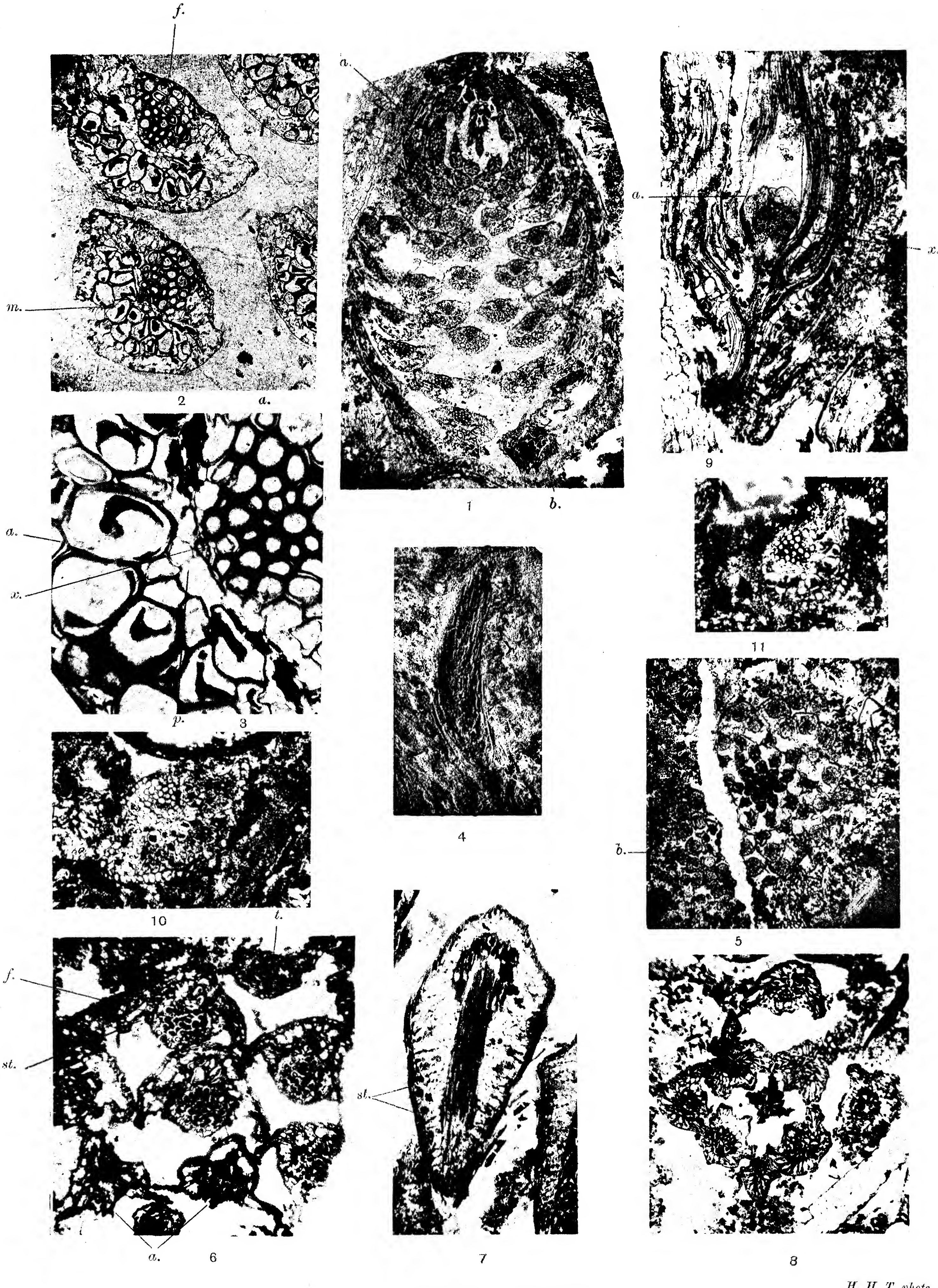
TWIGS AND YOUNG STEMS OF CALAMITES.

LEAVES OF CALAMITES.

H. H. T. photo.



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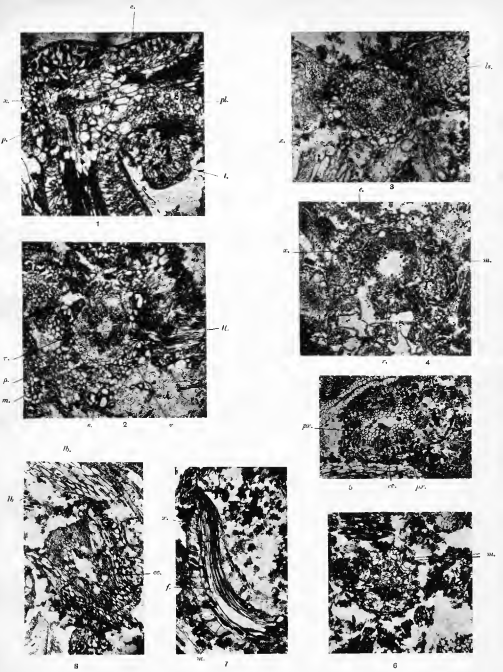

TWIGS AND YOUNG STEMS OF CALAMITES.

PLATE 3.

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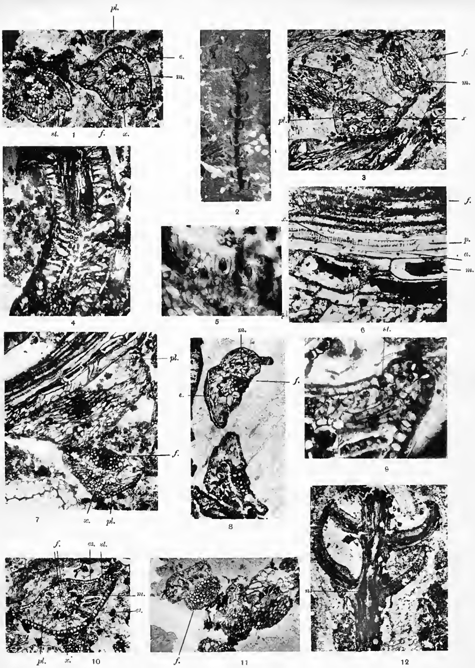

LEAVES OF CALAMITES.

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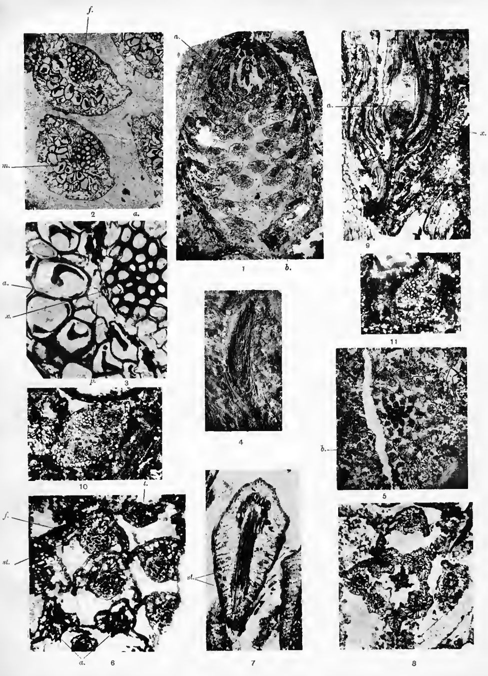

PLATE 5.

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